# Landscape – diversity relationships: ranking determinants of passerine species richness in the Vez watershed, Portugal


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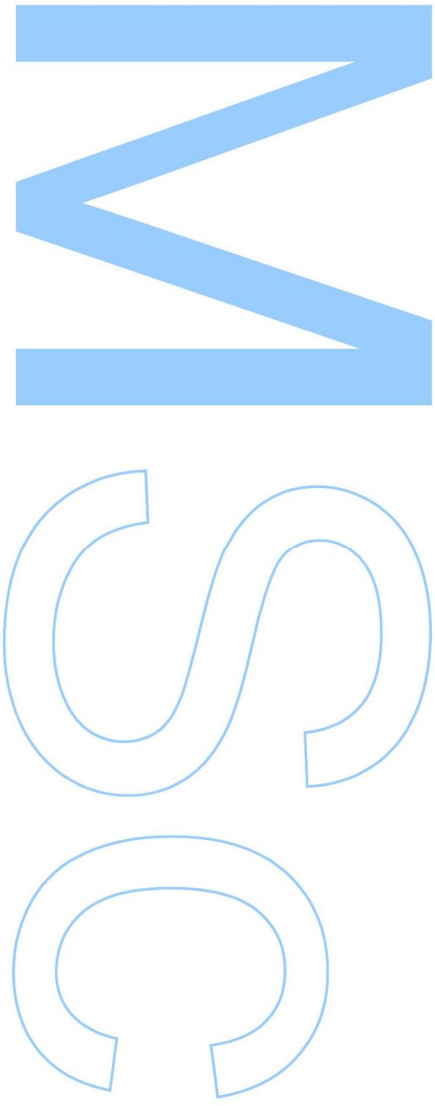

*Everything is connected to everything else,*

*Everything must go somewhere,*

*Nature knows best, and*

*Nothing comes from nothing.*

*The Four Laws of Ecology by*
*Barry Commoner in "The Closing Circle" (1971)*

## Abstract

Climate change and landscape dynamics are among the most prominent worldwide drivers of biodiversity loss. They are causing changes in landscape patterns and processes, leading to impacts on biodiversity and ecosystem functions by changing the distribution of suitable environmental conditions for many species. The accelerated loss of biodiversity and of the ecological services it provides has led to an increasing concern and recognition of the profound consequences for human wellbeing, highlighting the urgent need of measuring environmental change efficiently.

This study aimed to contribute to the improvement of conservation management by investigating the landscape ecological drivers of passerine diversity at the catchment level. A statistical modelling approach was developed and tested in the Vez watershed (NW Portugal), with the ultimate goal of establishing a framework capable of identifying groups of passerine species as indicators of the ecological state of the landscape.

To assess the relation of landscape-level species richness with a set of environmental factors (climate, topography, habitat diversity, habitat disturbance, landscape composition, and landscape structure), we used a modelling framework consisting of five steps. Models based on environmental variables expressing each group of ecological factors were developed by Generalized Additive Modelling (GAM), and then ranked using a Multi-model Inference framework, according to the Akaike's Information Criterion. We further assessed differences in model ranking for the whole species pool and for species groups based on habitat foraging and feeding traits. In order to control the potentially spurious sampling effort effect in models, we estimated the values for each response variable by fitting Species-Area Relationship (SAR), and then tested if this lead to an improvement of model performance.

Overall, the framework developed originated models with good performances. Results showed that SAR-estimated values allowed improving model performance, compared to directly observed values, thus minimizing the effect of differences in sampling effort. However, despite this difference, the two sets of models were congruent regarding the ranking of landscape ecological determinants. Landscape structure and habitat diversity were found to be the main determinants of variation in passerine species richness at the local scale. We also found that different functional groups respond to distinct drivers according to their ecological requirements. The presence of insectivorous species was highly correlated with (and promoted by) habitat diversity, while open area specialist species richness was strongly determined by landscape structure. In turn, granivorous species stood out by being the only group whose richness distribution was

mainly affected by habitat disturbance. Therefore, we suggest that these three groups may be used together as indicators of landscape ecological state in the Vez catchment.

Our results provide a more profound insight of the landscape conditions driving local biological diversity, and encourage the implementation of management strategies that promote habitat diversity and landscape heterogeneity. In addition, this study improved the understanding of the response of passerine species to landscape structure, disturbance and habitat change, which can help target and prioritize conservation and management efforts while informing on the ecological status of landscape mosaics.

**Key words:** Conservation, Generalized Additive Modelling, Landscape, Passerine birds, Portugal, Species richness, Vez catchment.

## Resumo

As alterações climáticas e as dinâmicas da paisagem estão entre as principais causas globais da perda de biodiversidade. Estas estão a causar mudanças nos padrões e processos da paisagem, o que afeta a biodiversidade e o funcionamento dos ecossistemas, e conduz à alteração da distribuição das condições ambientais adequadas para cada espécie. A perda acelerada de biodiversidade e dos serviços ecológicos que esta proporciona têm motivado uma crescente preocupação e reconhecimento das profundas consequências para o bem-estar humano, destacando assim a necessidade urgente em medir eficientemente as alterações ambientais.

Este estudo teve como objetivo contribuir para o melhoramento da gestão para a conservação através da investigação dos fatores ecológicos da paisagem que influenciam a diversidade de passeriformes ao nível da bacia hidrográfica. Uma abordagem de modelação estatística foi desenvolvida e testada na bacia hidrográfica do Vez (NW Portugal), com o intuito final de estabelecer uma moldura de trabalho capaz de identificar grupos de espécies de passeriformes como indicadores do estado ecológico da paisagem.

Para avaliar a relação entre a riqueza de espécies ao nível da paisagem e um conjunto de fatores ambientais (clima, topografia, diversidade de habitats, perturbação do habitat, composição da paisagem e estrutura da paisagem), foi usada uma moldura de modelação composta por cinco passos. Modelos baseados em variáveis ambientais representantes de cada grupo de fatores ecológicos foram desenvolvidas utilizando modelos Aditivos generalizados (GAM) e, posteriormente, hierarquizados usando Inferência multi-modelo, segundo o Critério de Informação de Akaike. Foram também avaliadas diferenças neste ranking entre a riqueza específica total e grupos de espécies baseados no seu habitat ou nos seus hábitos alimentares. De forma a controlar possíveis erros nos modelos motivados por diferenças no esforço amostral, foi estimado o valor de cada variável resposta utilizando a relação espécies-área (SAR) e testado o seu impacto na performance preditiva dos modelos.

Em geral, a abordagem desenvolvida originou modelos com boa performance. Os resultados revelaram que a utilização de valores estimados, em comparação com o uso de valores observados, melhora a performance dos modelos. No entanto, apesar desta diferença, ambos os conjuntos de modelos foram congruentes na classificação dos determinantes ecológicos da paisagem. Segundo os resultados, a estrutura da paisagem e a diversidade de habitats são os principais determinantes da variação da riqueza específica de passeriformes à escala local. Verificou-se, também, que diferentes grupos funcionais respondem a diferentes fatores, conforme os seus requisitos

ecológicos. A presença de espécies insectívoras apresentou uma estreita correlação com a diversidade de habitats, enquanto a riqueza de espécies características de áreas abertas foi determinada pela estrutura da paisagem. Por sua vez, espécies granívoras destacaram-se por serem o único grupo cuja distribuição da riqueza específica foi afetada principalmente por perturbações do habitat. Deste modo, é sugerido que estes três grupos possam ser utilizados como indicadores do estado ecológico da bacia hidrográfica do Vez.

Estes resultados proporcionam uma compreensão mais profunda das condições que promovem a diversidade biológica local, e incentivam a implementação de estratégias de gestão que promovem a diversidade de habitats e a heterogeneidade da paisagem. Além disso, este estudo aumentou o conhecimento sobre a resposta dos passeriformes à estrutura, perturbação e alteração da paisagem, o que pode contribuir para ajudar a identificar e priorizar esforços de gestão e conservação, ao mesmo tempo que fornece informação sobre o estado ecológico dos mosaicos da paisagem.

**Palavras-chave:** Conservação, Modelação Aditiva Generalizada, Paisagem, Aves passeriformes, Portugal, Riqueza de espécies, Bacia hidrográfica do Vez.

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## List of acronyms

**AIC** – Akaike Information Criterion

**AICc** - Corrected Akaike Information Criterion

**CBD** – Convention on Biological Diversity

**COS** – Carta de Ocupação do Solo

**DPSIR** – Drivers Pressures State Impact Responses

**EEA** – European Environment Agency

**GAM** – Generalized Additive Model

**GLM** – Generalized Linear Model

**GHC** – General Habitat Categories

**HCA** – Hierarchical cluster analysis

**ICNF** – Instituto da Conservação da Natureza e das Florestas

**MEA** – Millennium Ecosystem Assessment

**MMI** – Multi-Model Inference

**PSU** – Primary Sampling Unit

**REA** – Relatórios do Estado do Ambiente

**SAR** – Species-Area Relationship

**SSU** – Secondary Sampling Unit

**UTM** – Universal Transverse Mercator coordinate system

**VIF** – Variance Inflation Factor

# 1. Introduction

## 1.1. Global change factors and biodiversity reduction

Nowadays we are facing a severe global environmental change. Alterations include not only climate change (IPCC, 2014) but also land cover change, leading to landscape modifications that shape biological communities (Fischer and Lindenmayer, 2007; Tscharntke et al., 2012). Given the essential role of ecosystem services to human well-being provided by biodiversity (Millennium Ecosystem Assessment (MEA), 2005), forecasting and understanding the causes of variation and loss of biodiversity has been one of the fundamental aims of ecological research. It is currently attracting worldwide interest by researchers, politicians and the main public, evident by the establishment of World conferences (*e.g.* World Conference on Biodiversity in Nagoya 2010 and Hyderabad 2012) and international scientific councils (*e.g.* the "Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services IPBES") which highlight the importance and necessity to improve management and conservation plans (Sutherland et al., 2004b).

Changes in mean temperature and precipitation variability and extremes, increase of the intensity and frequency of disturbances (such as wildfires and storms), fragmentation and loss of habitats (mainly due to the development of urban areas and infrastructures) and the increase of human-mediated biological invasions are some of the consequences of the climate and land cover change phenomenon (MEA, 2005). These are also main drivers of biodiversity loss, along with the pollution of ecosystems by hazardous substances and the overuse and depletion of natural resources (Secretariat of the Convention on Biological Diversity & UNEP World Conservation Monitoring Centre, 2006).

According to the European Environment Agency (EEA), 60% of protected species assessments and 77% of habitat assessments recorded an unfavourable status. By 2050 the world population may rise beyond 9.6 billion, increasing most in the urban areas in developing regions (EEA, 2015), which will exert ever-increasing pressure on the ecosystems and their life-supporting services.

Climate change is considered one of the most important threats to terrestrial biodiversity, along with habitat loss due to land use change (Jetz et al., 2007; Newbold et al., 2015; Sala et al., 2000), promoting modifications of key ecosystem functions and often the depletion of ecosystem services (Bellard et al., 2012). The close relation between temperature and precipitation and energy availability and productivity has been

found to be a driver of biodiversity change by increasing the number of food resources and generating the ideal conditions (Correia et al., 2015; Evans et al., 2005b; Hawkins et al., 2003). Degradation and fragmentation are also well-known threats to global biodiversity (IUCN, 2014), and their effects are likely to be intensified under climate change (Bellard et al., 2012; Brook et al., 2008).

Changes in landscape composition (in reference to the different types and proportions of land cover) and configuration (*i.e.* the spatial arrangement of landscape elements of a given landscape matrix) lead to habitat loss by decreasing the size or shape of habitat patches which reduces the number of potential niches and, consequently, the receptivity for a great number of species (Bunnell, 1999; Walz and Syrbe, 2013). Changes in landscape structure may also increase the distance between habitat patches within the landscape (Goodwin and Fahrig, 2002; Öckinger and Smith, 2006) thus reducing its connectivity. Alterations in the spatial arrangement of a landscape affect its effectiveness, heterogeneity, connectivity and (consequently) functionality. Thereby, spatial and functional connectivity is an important determinant of survival and mobility of organisms, and thus the exchange of and between organisms (Schindler et al., 2013; Syrbe and Walz, 2012). In addition, the isolation of natural habitat patches is responsible for a decline of chances of species co-existence and, consequently, species richness (Tews et al., 2004). However, habitat heterogeneity can lead to increasing resource complementation, specially benefiting generalist species (Teillard et al., 2014).

These aforementioned landscape changes also impact habitat diversity (defined as heterogeneity rendered by different cover types, elements of the landscape and plant species (Fahrig et al., 2011)), which increases biodiversity (Schouten et al., 2009) either by providing resources and refuge for a wide arrange of species (Bennett et al., 2006; Dauber et al., 2003) or by preventing the dominance of a single superior competitor due to the partitioning of the resources (Huston and Huston, 1994).

Besides land cover change, wildfires are one of the major and most frequent agents of disturbance, being responsible for modifying landscapes around the world (Agee, 1996). As an example, in 2013, 19 291 fire events were registered in Portugal, resulting in around 152 756 hectares of burnt area, of which 36,4% occurred in forest areas and 63,6% in shrublands (Relatórios do Estado do Ambiente (REA), 2014). In 2006, 23,8% of the Vez watershed was burnt, and later, in 2010, despite the reduction, burnt area percentage was still 12.7% (National Cartography of Burnt Areas 1990-2012, ICNF). The impacts of these wildfires on biodiversity are determined by fire regimes.

Large fires are the cause of overall negative effects in diversity whereas fires of smaller scale can have beneficial effects (Moreira et al., 2001a; Moreira and Russo, 2007).

Despite being more relevant at different scales (global and regional, respectively), climatic and land use change influence each other and can have a synergistic effect (Opdam and Wascher, 2004), causing the change of landscape patterns and thus leading to an impact on future biodiversity and ecosystem processes by changing the distribution of suitable environmental conditions for most of the species. Therefore, many species will be forced to shift their distribution, in order to find more suitable habitat sites (to live, hunt, reproduce, among others), which results in regional species losses, *i.e.* the reduction of biodiversity.

### 1.2. Measuring and estimating species diversity

The loss of natural resources and the ecological services provided by them (Carpenter et al., 2006) led to an increase of global changing concern and recognition of the profound consequences for people lives, their economy, health and general well-being, highlighting the urgent necessity to measure environmental changes, using simple, resourceful and efficient measures, so action can take place. In order to achieve it, one of the first steps taken may consist of the measure of biodiversity.

Despite all the scientific advances (*e.g.* increasing number of developed tools and data sources) and the diverse ways to measure biodiversity, it is still not an easy task to do. Among them, one of the most common and perhaps the simplest one is measuring species richness, *i.e.* the number of different species in a given area. However, measuring all species richness would be a hazardous/impossible task given its complexity, the resources required to do it and the different nature/biology of species inhabiting a certain area. A solution to this problem was found in the use of indicator species.

An indicator species, as described by Landres et al. (1988) is *'an organism whose characteristics (e.g. presence or absence, population density, dispersion, reproductive success) are used as an index of attributes too difficult, inconvenient, or expensive to measure for other species or environmental conditions of interest'.*

Populating most terrestrial and marine ecosystems on earth, widespread, diverse and mobile, bird species are considered an important biodiversity indicator, since they are easy to identify, survey and census relatively to other taxa, and especially because they are sensitive to both anthropogenic and natural environmental change (Gregory and Strien, 2010). In addition, studies using birds are simplified due to extensive knowledge of methods of survey design and inexpensive count data assess (from either previous

records or volunteer surveys). Besides their visual and acoustic conspicuous presence in the ecosystem, bird species have high ecological importance, being responsible for an important number of ecological functions amid vertebrates. Among others they contribute to seed dispersion, predation, pollination, nutrient cycling (via scavenger birds, for example) and nutrient deposition (Sekercioglu, 2006).

Some birds' taxa are good ecological indicators providing useful whole-system information, such as by capturing species diversity trends in face of disturbances (Carignan and Villard, 2002) or, when expressed as guilds or traits, by reflecting the trophic responses to land use gradients of change, both in composition and functioning terms (Santos and Cabral, 2004; Vandewalle et al., 2010). This is, for instance, the case of passerine communities, which exhibit several characteristics that justify their relevance as ecological indicators: (1) they are placed at an intermediate functional position in food webs (*e.g.* Herrando et al., 2005), (2) they provide cheap and easy measurements if standard methodologies are applied (Sutherland et al., 2004a), (3) they are sensitive to landscape and climatic patterns and changes (*e.g.* Regos et al., 2015), (4) several species were studied intensively with regard to their natural variation (*e.g.* Martin et al., 2006), and (5) they have the capacity for population recovery in response to good management procedures in previously disturbed ecosystems (*e.g.* Perkins et al., 2011).

Finally, birds have a close proximity with all people and their day-to-day activities (either recreational or work related) being a constant presence visually (*e.g.* flying over your car) or aurally (*e.g.* singing in the morning) (Whelan et al., 2008), which can be a useful bridge – that other taxa don't have – when raising awareness of biodiversity loss and its impacts (Gregory and Strien, 2010).

Decisions on biodiversity conservation and the design of effective conservation policies requires a great knowledge on species distribution (Whittaker et al., 2005). Most commonly, this representative data acquisition is obtained via field work, which requires numerous resources (human and material) and funds. However, due to (mainly) economic crisis and budget deficits, this task is facing an increasingly scarce funding (Gardner et al., 2008), which revealed a necessity to find other alternatives, as efficient and less resource-consuming. Data stored in museums, atlas, and unpublished material emerged as an efficient alternative (Graham et al., 2004).

Nevertheless, the sampling effort of the aforementioned data sources can be biased due to, among others, differences in sampling effort, the number or size of areas visited and the number of collecting expeditions, which can compromise biodiversity

analysis and conservation planning (De Ornellas et al., 2011; Rocchini et al., 2011). Therefore, studies involving the comparison of species richness between different areas need a suitable control of data-quality in order to mitigate the errors (Hortal et al., 2007), as well as some form of species richness 'standardization', such as extrapolation or rarefaction techniques (Gotelli and Colwell, 2001; Walther and Martin, 2001; Walther and Moore, 2005).

In recent years, much focus has been directed to the development of these new methods to correct for sampling bias in the estimation of spatial and temporal variation in species richness (Colwell et al., 2012; Ibáñez et al., 2006). One solution resides in the use of species richness estimators. By providing unbiased measures of species richness that minimize measurement errors and improve the analysis of biodiversity patterns, these estimators can be used to standardize the effects of uneven sampling efforts (Borges et al., 2009; Hortal et al., 2004). Its use originated numerous methodologies that can be distinguished in four different groups according to Hortal et al. (2006): nonparametric estimators (Rosenzweig et al., 2003), fitting species-abundance distributions (Colwell and Coddington, 1994), species accumulation curves (Jiménez-Valverde and Lobo, 2005) and species–area curves (Ugland et al., 2003). The latter is one of the main tools used for extrapolation, resulting from the species-area relationship, one of the most ancient and robust "genuine law" of ecology (Holt et al., 1999; Schoener, 1976), which consists on the tendency for species richness to increase with sampled area. Despite this increase, when regressing species numbers against area, the relationship is not linear but instead presents a curve, usually nonasymptotic, that allows the extrapolation of the number of species that can be expected to be found at a given (limited) area size (Hortal et al., 2006).

### 1.3. Modelling biodiversity

Species richness, the simplest measure of species diversity, and its patterns have been intensively studied and various hypotheses have been formulated regarding the factors influencing broad to local scale gradients. Overall, exploring the relationship between species richness and environmental variables can provide a more profound insight of the landscape conditions leading to biological richness and improve the prediction of the response of species to landscape disturbance and habitat change (Orme et al., 2005).

Taking into account the difficulty in obtaining records of the distribution and abundance of the world species and since there is still no complete inventory of this data (as previously mentioned), the use of models became a common and viable tool to obtain

and apply information regarding the distribution patterns of biodiversity in space and time (Raven et al., 2002).

After formulating several theoretical explanatory hypothesis of how environmental factors determine the distribution of species and communities (Bar-Massada et al., 2012), a mathematical basis for interpretation can be provided using statistical models. These models are a mathematical simplification and an approximation of the reality that contributes to quicken and deepen the understanding of the ecology of a species or group of species and allow the examination of diverse parameters, namely the fit and strength of association between a response variable (*e.g.* bird species presence, abundance or diversity (Bergen et al., 2007)) and the explanatory variables (*e.g.* temperature, precipitation) (Guisan et al., 2002). Even though the result may not be entirely correct, due to the inherent complexity of Nature, it gives a direct tool to apply (among others) in conservation planning (Moilanen et al., 2009).

Generalized Linear Models (GLMs) and Generalized Additive Models (GAMs) are the most frequently used regression methods in ecology. Both are based on an assumed relationship between the mean of the response variable and the linear combination of the explanatory variables. However, despite being mathematical extensions of linear models, GAMs are more flexible and more adjusted to analyzing ecological relationships since they allow for non-linearity and non-constant variance in the data (Guisan et al., 2002; Hastie and Tibshirani, 1990). As semi-parametric extensions of GLMs, GAMs present a better approach to model highly non-linear data structures, given their assumption that functions are additive and the components are smooth. Rather than assuming a parametric relationship (Yee and Mitchell, 1991), it is the data that determines the nature of the relationship between the response and explanatory variables. This feature makes these models more data-driven, and, consequently, more adequate to represent ecological systems (Guisan et al., 2002).

When describing the relationship between environmental features and species richness, habitat attributes are widely used as predictive variables (Guisan and Zimmermann, 2000) as well as landscape metrics describing and quantifying the spatial patterns of habitats (McGarigal et al., 2012). More specifically, these variables allow the description of the species' habitat through characteristics such as the composition, spatial configuration, diversity and disturbance, which are in constant transformation due to changes in land use and climate, as previously described.

The relative importance of these factors (*e.g.* climate, habitat diversity/heterogeneity) is scale-dependent. While at the local extent, a wide range of biotic and abiotic factors (*e.g.* plant species diversity, percentage cover of natural forest)

are important, at landscape extents climatic and historical factors dominate (Willis and Whittaker, 2002). Several examples also show how differences in scale can influence variables' contribution to regression models of species richness (Allen H. Hurlbert and John P. Haskell, 2003).

In addition, animal movements differ at diverse spatial scales depending (among others) on their use of the landscape (*e.g.* for foraging or breeding) or their use of different habitats to find temporally various resources (Holland et al., 2004; Mac Nally and Horrocks, 2000; Pope et al., 2000). Their ecology affects how they perceive area and objects in the landscape which is thought to determine their use of that habitat. As a result, the effects of landscape change on birds' functional groups are the result of their extent combined with adaptations species have achieved during their history when facing these changes (Covas and Blondel, 1998).

Even though landscape characteristics have been known to affect the distribution of species richness, having been the focus of many studies (*e.g.* Evans et al., 2005a; Joaquín Hortal et al., 2009; Lindenmayer et al., 2014; Schindler et al., 2013; Wretenberg et al., 2010), researches frequently focus on the effect of only one or two landscape characteristics (*e.g.* Carrara et al., 2015; Schouten et al., 2009) or, in other hand, effects are scrutinized in a combined fashion in modelling or analysis, disregarding their independent effect (*e.g.* Seoane et al., 2013) and with no *a priori* hypotheses being defined. Thus, little is known about the independent importance of each characteristic when compared to others. This knowledge, regarding how organisms select its habitat and at what level they respond to landscape characteristics, can be essential when facing budget and/or time constraints for conservation measures, define management priorities or to predict the outcome of a given land use change scenario.

### 1.4. Biodiversity conservation

Nature reserves and protected areas are currently being created worldwide in order to protect species and ecosystems from the harmful human activities and its consequences (Mittermeier et al., 2003). According to the European Red List of Birds (BirdLife International, 2015), 13% of wild bird species regularly occurring in Europe are currently threatened, and 6% are Near Threatened.

Due to the failure of the previous goal (to halt the biodiversity loss by 2010), in 2010 the Parties to the Convention on Biological Diversity (CBD) adopted a revised and updated Strategic Plan for Biodiversity (Aichi-Nagoya COP 10 CBD, 2010), setting as its main objective to halt the loss of biodiversity and degradation of ecosystem services in the EU by 2020 (REA, 2014). It includes various goals, among which are limiting the

deterioration of the conservation status of all species and habitats covered by EU legislation (and improve them significantly), so that, by 2020, comparatively to current evaluations: a) more than 100% of habitat evaluations and 50% of evaluation of species under Habitats Directive show an improved conservation status and b) more than 50% of evaluations of species under the Birds Directive show a secure or improved status (REA, 2014).

There are many ways to approach landscape conservation and develop effective conservation strategies. However, ecological knowledge often fails to be applied and adopted on sites (Fazey et al., 2006). Lindenmayer et al. (2008) suggested a set of important issues that should be considered by managers and agencies when developing conservation plans. Among them is the importance of using an appropriate landscape conceptual model and managing landscapes in an adaptive framework. Also, it stresses the importance of landscape classification, the determination of habitat amount, amount of land cover, patch sizes and mosaics, assessing connectivity and edge effects and the necessity to set long-term ecological goals.

In addition, a diverse number of management strategies can be applied to conservation plans (Lindenmayer et al., 2008), common examples being the protection of focal species (the most susceptible) in an attempt to link landscape patterns and the ecology of species, and the protection of species-richness hotspots (Mittermeier et al., 1998). Regardless of the method used, they all have strengths and weaknesses that must be accounted for when structuring a conservation plan. Some of the weaknesses consist on the lack of representativeness of methods based on single-species models (which are frequently the focus on literature) due to the multitude of existing species in a landscape and the fact that most approaches don't explicitly recognize uncertainty, which increases with larger landscapes and longer time spans (Burgman et al., 2005). However, the uncertainty can be assessed by careful evaluating model predictions and by monitoring (over time) the consequences of management decisions and posteriorly improve them. In general, landscape management requires an adaptive and thoughtful process in order to maximize performance (Westphal and Possingham, 2003) and by using more robust outcomes, decision strategies become appealing to the stakeholders (Burgman, 2005).

Complexity, structure or level of detail of the models used depend on the necessary decisions to be made. Better decisions don't always depend on the more precise and scientifically true models, but rather on the ones that lead to more robust and context driven decisions (Pielke Jr, 2003). Resorting to only science-based considerations can,

sometimes, reveal to be impossible due to political and/or social restraints (Bürgi and Schuler, 2003).

In order to develop effective conservation strategies is necessary to acquire sufficient knowledge of the spatial distribution of species richness since the identification of areas highly valuable and diverse in terms of species richness can contribute to the optimization of conservation efforts in response to limitations like knowledge, space, time, and money (Myers et al., 2000), which meets the political and economic demands currently made.

In turn, by being able to identify patterns in species richness and the fundamental environmental factors underlying these patterns, we can derive the requirements to efficiently protect biodiversity, which shows that a general understanding of the species richness-environment relationship is also very important (Williams et al., 2002) .

**Main objectives**

This project aims to contribute to the improvement and simplification of conservation efforts by investigating landscape ecological drivers of passerine diversity patterns and by establishing a framework capable of generating the identification of group indicators of the ecological state of the landscape.

Thus, the objectives of this study were:

i) Understand passerine species richness' distribution along the study area;

ii) Investigate and rank the landscape drivers of passerine species richness at the local scale, using regression models;

iii) Assess ranking differences between total species richness and species richness by habitat foraging and feeding traits;

iv) Assess if estimated data based on Species-Area relationship can improve model performance;

v) Use model ranking to select indicator groups based on different responses to environmental drivers;

vi) Based on modelling results provide contributions for adaptive management and improve conservation policies at local level.

This will be examined in the Vez watershed, in the North of Portugal, representing a major climatic and ecological contrast in the region.

# 2. Methods

## 2.1. Study area

The study area is located in the medium-sized watershed of river Vez (252 $Km^2$), in the Soajo and Peneda mountains, northwest Portugal (bounded by -8.526°W to -8.257°W longitude and 41.837°N to 42.017°N latitude) (Figure 1, a, b). The Vez river is one of the main tributaries of the river Lima, a major river in the northwest Iberian Peninsula. Annual precipitation in this area ranges from 1000 mm/year in lowlands up to 3000 mm/year in highlands, occurring mainly during the autumn and winter months (*Instituto Português do Mar e da Atmosfera - IPMA*). In the lowlands, the climate presents a Mediterranean type of rainfall regime, whereas in highlands rainfall seasonality is softer and the climate is considered Temperate Atlantic with a sub-Mediterranean regime (Mesquita and Sousa, 2009). In terms of average annual precipitation and average annual temperature these are 1500 mm/year and 13.8 ºC, respectively.

This area holds important biodiversity values, being 13.6% included in the only Portuguese National Park (Peneda-Gerês) and 43.3% classified as Natura 2000 protected site. This area has a complex topography with elevation ranging from 30 m to 1400 m and with 58% of the watershed having a slope above 25% (Figure 1, c). Regarding the dominant land cover types, highlands are characterized by open areas of bare rock and heath, scrubland (broom) and transitional forest areas, which are mostly coincident with the Peneda-Gerês National Park, whereas agricultural and forest areas (common oak, maritime pine, and eucalyptus) are more common in lowlands (Caetano et al., 2009). Overall, this is a highly diversified and dynamic landscape that has been shaped by a marked rural abandonment and afforestation in the last two decades, with anthropogenic fires playing an important role as drivers of landscape change (Moreira et al., 2001b).

With respect to the regional geology, granites and schist are characteristic, and the major soil types are: Humic Regosols (67%) and Leptosols (9%) prevailing in highlands; Dystric Antrosols (22%), Fluvisols (1%) and Urban (0.56%) in lowlands.

Regarding social occupation, this area presents dispersed low-density human settlements around the main water courses and roads with the center of the villages having more concentration of habitation and other buildings.

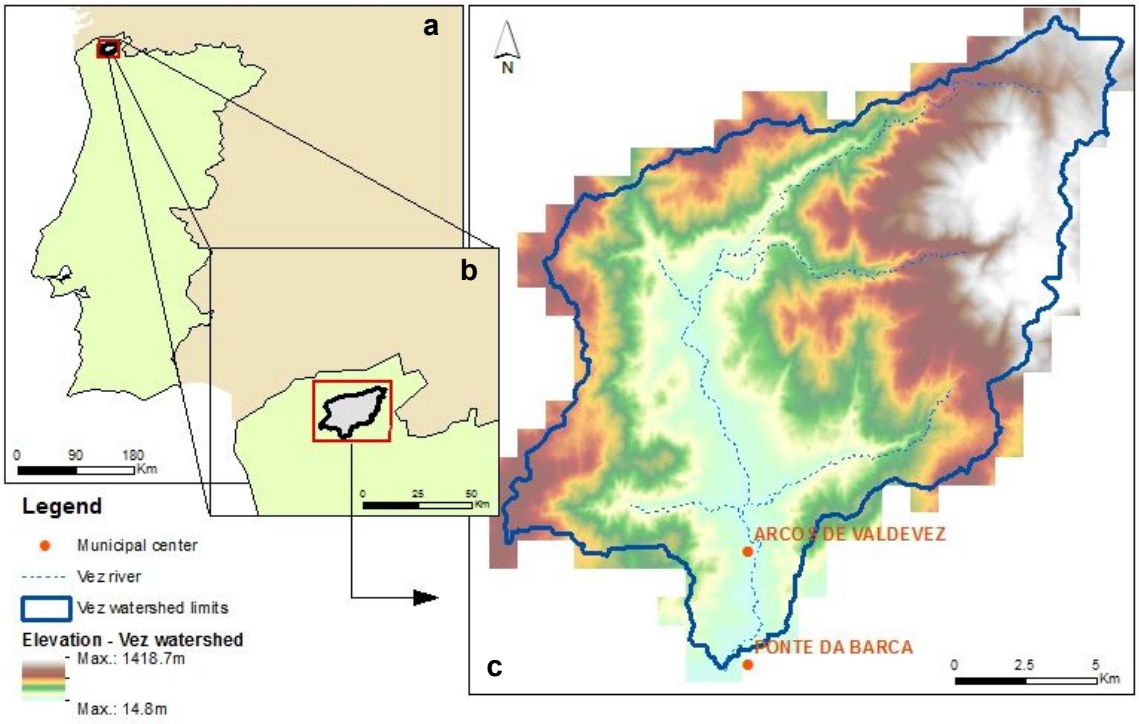


Figure 1 – Location (a, b) and topography map (c) of the study area in NW Portugal.

### 2.2. Sampling design

Prior to field surveying of birds, a two-stage sampling design was implemented to select sample locations. This design had, primarily, the purpose of selecting a set of locations from which scientifically valid inferences could be made and the definition of the sample size, area and shape of sample units.

In the first stage of the sampling design, a stratified random sampling approach was used to select Primary Sampling Units (hereafter PSU), registered in a regular grid with 1km$^2$ square units (Figure 3). Stratification data (including climatic and topographic variables, soil types and the distribution of protected areas) that were used to divide the study area in sub-areas (Figure 2), called 'strata', in each of which is applied simple random sampling – the sampling units are selected at random from the units comprising the study area in order to guarantee the same selection probability to all possible distinct units. This stratification, which is an essential first stage to better understand ecological patterns and processes (Jongman et al., 2006), aims at forming groups of sample units with similar environmental characteristics. The development of the stratification of the study area was supported by concepts related with the DPSIR causal framework (adopted by the European Environment Agency), which is used to describe the interactions between society and the environment and helps to structure information and

to identify important relations (Ness et al., 2010). The scheme comprehends the following components: driving forces (D), pressures (P), system states (S), impacts (I) and responses (R). Other components linked with the systems' abiotic conditions (C) (mainly describing climate, topography and soil conditions), the systems' wildfire regime and variables related to the nature protection regimes were also considered.

Due to a large number of climatic and topographic variables available we performed a Principal Component Analysis which allowed the reduction of the number of variables while maintaining the most important gradients by selecting variables highly correlated to each of the 6 initial principal components.

All the variables used in the development of the Vez watershed stratification and its relation with DPSIR concepts are listed in table 1.

Table 1 – Variables used in the development of the Vez watershed stratification and its relation with DPSIR concepts.

| ***Type (DPSIR)*** | ***Variables description*** | ***Dataset*** |
|---|---|---|
| Conditions (C): Climate | Temperature Annual Range (ºC) | WorldClim – Bioclimatic variables (Hijmans *et al*. 2005) |
| | Precipitation of Driest Quarter (mm) | |
| Conditions (C): Topography | Slope (in %; mean value for the 1km$^2$) | IGeoE série 1:25000 |
| Conditions (C): Soil type | Cover of antrosols (%)<br>Cover of fluvisols (%)<br>Cover of leptosols (%)<br>Cover of regosols (%) | Carta de Solos de Entre Douro e Minho |
| DPSIR / Pressures (P) | Average 1990-2012 burnt area percentage in each 1km$^2$ | Cartografia Nacional de áreas ardidas 1990-2012 / ICNF |
| DPSIR / Responses (R) | Cover of Protection Level 0 (no protection status) (%)<br>Cover of Protection Level 1 (only one of these conservation status: Natura 2000 SAC's or Natura 2000 SPA's or areas in the National Network of Protected Areas – NNPA) (%)<br>Cover of Protection Level 2 (a combination of two conservation status: SAC/SPA, SAC/NNPA or SPA/NNPA)<br>Cover of Protection Level 3 (combination of all three conservation status: SAC/SPA/NNPA) | Cartografia da Rede Nacional de Áreas Protegidas e Rede Natura 2000 / ICNF |

Finally, in order to obtain the stratification, we used cluster analysis with the best clustering solution being the PAM algorithm for a total of 6 clusters (or strata) with an Average Silhouette Index of approximately 0.53.

A total of 24 primary sample units (PSU's) were selected with allocation proportional to stratum area and a minimum of three per strata (figure 3).

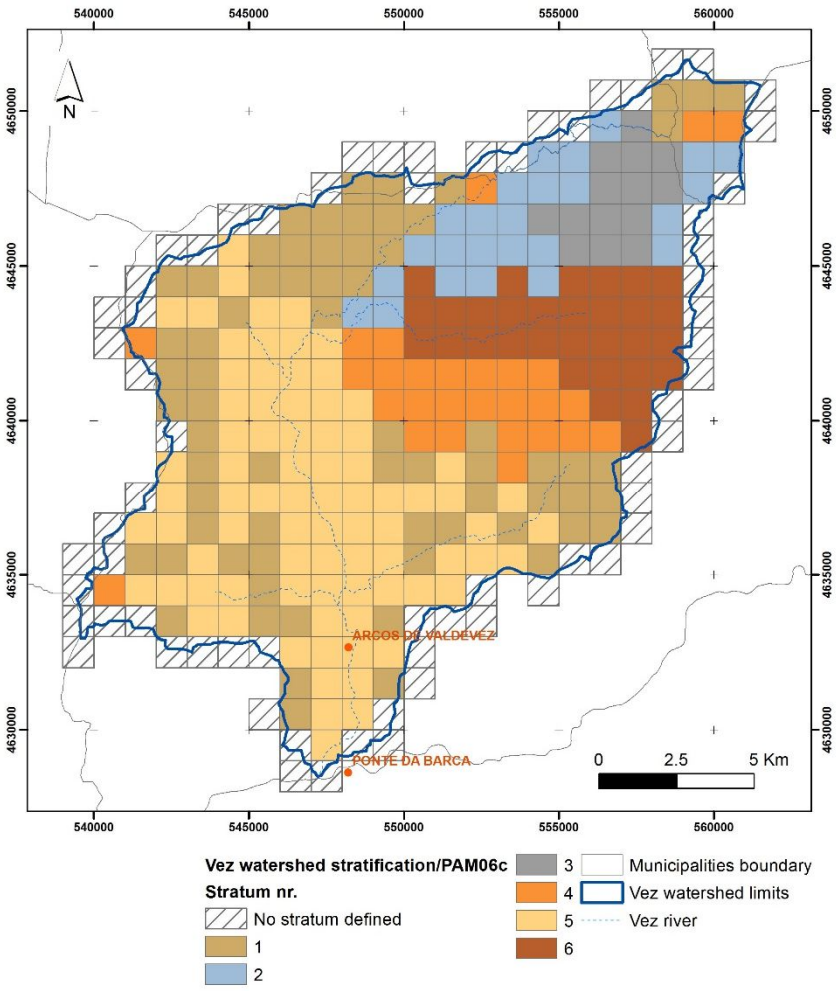


Figure 2 – Vez watershed stratification with 6 strata generated by the PAM algorithm used in the stratified random sampling approach.

In a second stage, with the purpose of defining sample units for surveying bird diversity and allowing to reduce overall sampling costs of the entire 1×1km PSU area, we used a systematic sampling approach to select five Secondary Sampling Units (hereafter SSU's). Each SSU had an area equal to 0.04km$^2$ (200×200m) located at the corners and the centre of each PSU (Figure 3). A total of 120 SSU's were initially selected using systematic sampling, however only 111 from the initial set were surveyed given that nine units were not possible to access due to the absence of roads, tracks or due very dense vegetation cover in the area.

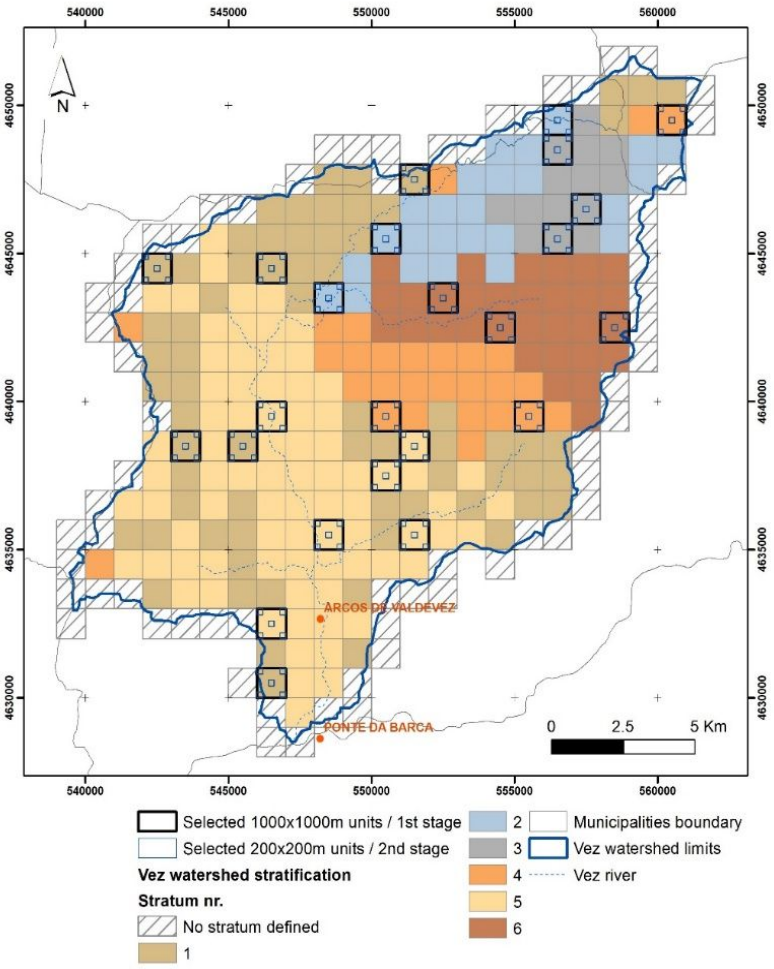


Figure 3 – Vez watershed sample locations selected using the adopted two-stage sampling design for a sample size of n = 24.

### 2.3. Bird surveys

In order to obtain estimates of passerine bird species richness (number of different species represented in each 1km$^2$ sampling unit) in the study area we carried out a bird census in spring of 2014, from early May to mid-June, during breeding season, using point-count sampling (Bibby, 2000). This method consists of standing in a specific location and counting birds seen or heard within a circle of a certain radius for a predetermined and limited time. It is a simple, efficient and inexpensive method, which requires few subjective decisions by the observer, and it is easily reproducible in different times or places (Howe et al., 1997). When used, it allows the estimation of relative abundance and population trends (*i.e.* species diversity/richness, population size/density) between different periods of time (*i.e.* seasons or years) or during the

changing of habitat area. The counting period of each sampling unit can vary between different studies (Ralph et al., 1995), being a compromise between the acquisition of an accurate representation of the birds' presence and the increase of the statistical power of the effort by sampling a larger number of units and birds (Verner, 1988).

We conducted a 100m fixed-radius point-count surveys (Bibby, 2000) in the 111 SSU´s (with an area of 0.04 $km^2$) (Figure 4), in which all the birds heard or seen in a ten-minute period were recorded. Point-counts were performed at the plot centroid and separated by at least 565m to the nearest survey location of the same PSU in order to minimize the probability of sampling the same birds more than once. Survey locations were visited once by the same two well-trained persons to avoid between-observer variations and were all conducted within the first 3h of the morning and in the afternoon beginning 2h before sunset. This period of time coincide with the peak of bird activity (more movements and singing and calling behaviors) which leads to the recording of the maximum birds' presence in a short period of time (Bibby et al., 1998).

In each census, the sampling unit code, the date and hour, maximum and minimum temperature and precipitation were also recorded. During windy and rainy days we did not conducted the surveys since it may decrease bird's detection about 10% (Ralph et al., 1995).

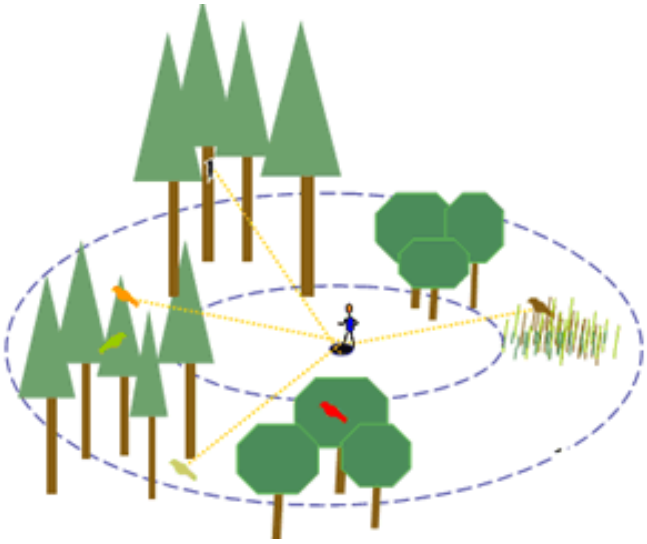

Figure 4 – Schematic representation of the point-count bird survey (source: http://www.pwrc.usgs.gov/point/index.cfm?fa=pointcount.whatIsAPointCount).

### 2.4. Habitat surveys

During May and July 2014 a comprehensive habitat survey was also performed in the SSU's. This survey followed the '*Manual for Habitat Surveillance and Monitoring and Vegetation in Temperate, Mediterranean and desert Biomes*' (Bunce et al., 2011) and the General Habitat Categories (GHC) classification system, resulting from several projects financed by the European Union , such as the BIOHAB-a framework for the coordination of biodiversity and habitats (www.edinburgh.ceh.ac.uk/biota/biohabpage.htm) and the European Biodiversity Observation Network (EBONE, http://www.ebone.wur.nl). According to the definition used in this manual (described by Bunce et al. (2008)), habitat is: "*an element of land that can be consistently defined spatially in the field in order to determine the principal environments in which organisms live"*. To enable the recording of ecosystems or habitats in a consistent manner, the authors developed General Habitat Categories (GHCs), which are mainly based on Plant Life Forms (LF; Raunkiaer, 1934) with added qualifiers on environment, site, management, species composition and non-Life Form Habitats (NLF) such as crops and sparsely vegetated land. This survey, performed by teams of two experienced investigators (a botanist and a GIS expert), allowed the recording of all life forms and non life-forms categories present in each SSU with a cover of over 10%, as well as the plant species present with significant cover.

### 2.5. Variables description

#### 2.5.1. Response variables

***Observed species richness***

After the bird survey, we calculated the passerine species richness for each primary sampling unit (PSU; 1 $km^2$). We did so by summarizing the total number of different passerine species in each SSU and aggregated it to its respective PSU.

We also grouped the passerine species into functional groups based on their feeding habits and habitat preferences. Regarding their diet, we considered three groups characterized according to their relative degree of functional specialization on insects, seeds or both (Catry et al., 2010): granivorous (*i.e*. those with a substantial seed component in the diet), insectivorous (*i.e*. those which diet consists primarily of insects) and omnivorous (*i.e.* those with a diet that includes both seed and insects).

The passerine species were also organized into three foraging habitat trait groups (which were assumed as indicators of the potential ecological cause-effect relationships induced by land use patterns and change (Moreira et al., 2001a): species that inhabit

mainly woodlands, species that inhabit mainly shrublands and species that inhabit mainly open areas (including an array of different land use/cover types such as farmland mosaics, grasslands and/or sparsely vegetated mountainous areas). This organization was obtained by using data from literature taking into account the main habitats that characterize the study area: woodlands, shrublands and grasslands (Gil-Tena et al., 2009; Moreira et al., 2001a; Regos et al., 2015).

The species richness of each functional group was calculated by adding the number of recorded species belonging to each group by PSU (1km$^2$ units).

***Estimating species richness using Species-area curves***

Since some PSUs were not completely surveyed, due to constraints in accessing all five nested SSUs, this caused some unevenness in sampling effort across different primary units. In order to minimize this problem, potentially adding a spurious sampling effort effect in models, we estimated values for each response variable by fitting Species-Area Relationship (SAR) curves implemented in the *mmSAR* package in R (Development Core Team, 2012; Guilhaumon et al., 2010). This relationship consists of the change in species numbers with increasing area and is commonly used to establish patterns of biodiversity that support biologic conservation efforts (Guilhaumon et al., 2008). The *mmSAR* package uses a comprehensive set of SAR models, including five convex models (power, exponential, negative exponential, Monod and rational function) and three sigmoid models (logistic, Lomolino, and cumulative Weibull), in order to encompass the various shapes attributed to SARs in the literature (Guilhaumon et al., 2010).

The modelling procedure used the scaling properties of SAR for estimating total passerine species richness and passerine species richness by trait group (feeding and habitat preference) for each PSU based on data from one up to the five nested SSUs. Species-area curves were fit using the resampled average number of species (for 100 repetitions) for 0.04km$^2$ (one SU), 0.08km$^2$, 0.12km$^2$, 0.16km$^2$ and 0.20km$^2$ (five SSUs, i.e., considering all SSUs nested in a given PSU). Model fitting employed the eight models currently implemented in the *mmSAR* package. Models were then combined and multi-model averaged predictions were obtained for the entire PSU with a target area of 1.00km$^2$. By averaging these models, the package allows the construction of robust inferences that incorporate the uncertainty regarding both model selection and parameter estimation (Guilhaumon et al., 2008). The graphics representing the obtained SAR curves for each PSU are presented in appendix I.

Models obtained with observed and estimated values of species richness were compared both in terms of predictive performance and consistency to rank each tested hypotheses.

A total of seven response variables summarizing the data collected during bird surveys and regarding passerine communities at PSU level (1km$^2$) and seven SAR- estimated response variables (table 2) were used in the modelling framework (chapter 2.6.2.).

Table 2 – Code name and description of the response variables used in the modelling framework.

| | Code name | Variables Description |
|---|---|---|
| Observed species richness | SpRich.ObsField | Observed passerine species richness |
| | Feeding.I.ObsField | Observed number of insectivorous species |
| | Feeding.G.ObsField | Observed number of granivorous species |
| | Feeding.O.ObsField | Observed number of omnivorous species |
| | Foraging.O.ObsField | Observed number of open areas specialist species |
| | Foraging.S.ObsField | Observed number of shrublands specialist species |
| | Foraging.W.ObsField | Observed number of woodlands specialist species |
| Estimated species richness (using SAR curves) | SpRich.multiSAR | Estimated passerine species richness |
| | Feeding.I.multiSAR | Estimated number of insectivorous species |
| | Feeding.G.multiSAR | Estimated number of granivorous species |
| | Feeding.O.multiSAR | Estimated number of omnivorous species |
| | Foraging.O.multiSAR | Estimated number of open areas specialist species |
| | Foraging.S.multiSAR | Estimated number of shrublands specialist species |
| | Foraging.W.multiSAR | Estimated number of woodlands specialist species |

### 2.5.2. Predictive variables

In order to determine the main drivers of passerine species richness in the study area, a set of predictive variables were used.

Bioclimatic variables (calculated based on precipitation and temperature data) were obtained from the WorldClim data set (Hijmans et al., 2005). Variables summarizing topographic features (related to slope and elevation) of the sampling plots were calculated from 1:25.000 elevation data (including contour lines and point elevation) of the Portuguese Instituto Geográfico do Exército (IGeoE).

For characterizing ecosystem disturbance related to wildfires, we used the National Cartography of Burnt Areas 1990-2012 provided by ICNF (*Instituto da Conservação da Natureza e das Florestas*) we calculated the average 1990 - 2012 burnt area percentage in the sampling units, separated in three different periods of time: 13 years (between 1990-2012; the complete temporal extent of the database), 10 years (between 2003-2012) and 5 years (between 2008-2012).

For evaluating disturbances related to land use/cover change, the Portuguese Land Cover Map *'Carta de Ocupação do Solo (COS) 2012*' (Direção-Geral do Território ESA/IPVC, 2014; with a Minimum Mapping Unit of 1ha) was used to calculate the percentage cover of areas that have suffered a change in land cover/use category between 1990-2012 using ArcGIS 10.1 software (ESRI, Redlands, CA). This map was primarily produced in 1990 by the Portuguese Geographic Institute (URL: http://ftp.igeo.pt/produtos/CEGIG/COS.htm) and posteriorly updated for the study area, in 2000 and 2012, by *Escola Superior Agrária* of *Instituto Politécnico de Viana do Castelo* as part of the IND_CHANGE project.

In order to characterize different aspects related to landscape composition we calculated (using ArcGIS 10.1 software (ESRI, Redlands, CA)) the percentage covered by different land cover categories in each sampling unit, we also used data obtained from the Portuguese land cover map *'COS 2012*' (ESA/IPVC, 2014), for the following habitat land use/cover classes:

- Annual crops – crop areas whose growth season does not exceed one year or are replanted in intervals of less than five years, which guarantees an annual or multiannual rotation regime. It includes watered and non-watered crops, crops in flooded fields (*e.g.* paddy fields), temporary pastures and fallow lands.
- Bare rock and sparsely vegetated areas – areas with little vegetation (less than 10%) whose surface is covered more than 90% by rock. It includes shed deposits, escarpments and rocky outcrops.
- Built-up areas – built areas of urban typology (houses, buildings, car parks, playgrounds, roads, etc). These surfaces are highly waterproofed and have little or no vegetation.
- Natural forest – Areas covered mainly by deciduous forest (*e.g. Quercus robur*) and riparian forest (*e.g. Alnus glutinosa, Fraxinus excelsior, Salix sp.*)
- Permanent crops – crop areas that occupy the land during long periods of time while providing multiple crops without applying the rotation regime. Orchards, olive groves (with minimum density of 100 trees/ha and 45/ha, respectively) and vineyards for production are included in these class, unlike meadows and permanent grasslands.
- Production forest – Areas covered essentially by Eucalyptus forest (*Eucalyptus sp.*), Pine forest (*Pinus pinaster*) or a mixture of the two.
- Scrublands and heathlands – Natural and semi-natural areas covered by evergreen scrub or heath (possibly including recently burned areas and areas with some natural forest regeneration).

Using *'COS 2012'* data we also calculated other indices of habitat diversity/heterogeneity for each PSU by calculating Shannon's diversity index.

To further complete the characterization of surveyed plots we calculated habitat type richness as well as plant species richness, by summarizing all the GHCs and plant species, respectively, registered in each SSU during habitat surveys.

The landscape structure of the study area was also assessed by calculating several landscape configuration variables, portraying different aspects of the spatial patterns of the landscape related to patch area and edge, aggregation, shape and core area. Area and edge metrics consider the size of the landscape's patches and the total edge created by them. These metrics consist of the area (AREA) and extent (GYRATE) of each patch, the total edge (TE; *i.e.* the length of all patch types present in the landscape), the edge density (ED), which standardizes TE to a per unit area basis and the Largest Patch Index (LPI) which is a measure of dominance, quantifying the percentage of total landscape area comprised by the largest patch.

Shape metrics translate the features of patch shape by measuring its complexity compared to a standard shape (square) of the same size (SHAPE), the perimeter-area ratio (PARA), the perimeter-area fractal dimension (PAFRAC), the Fractal dimension index (FRAC), the spatial contiguity of cells within a grid-cell patch (Contiguity index; CONTIG) and the ratio of patch area to the area of the smallest circumscribing circle (related circumscribing circle; CIRCLE). Core area metrics (*i.e.*, the area within a patch without depth-of-edge influence), like patch shape, are closely related to the 'edge effect' (Hansen and di Castri, 1992), and measure: core area distribution (CORE), total core area (TCA), number of disjunct core areas (NDCA), disjunct core area distribution (DCORE), disjunct core area density (DCAD) and Core Area Index Distribution (CAI). The Core area index is a relative index that quantifies the percentage of the patch that is comprised of core area. Finally, aggregation metrics refer to the tendency of patch types to be spatially aggregated, describing the closely related concepts of dispersion, interspersion, subdivision and isolation. These metrics measure the number of patches (NP), patch density (PD), landscape division index (DIVISION), Patch Cohesion Index (COHESION), Contagion (CONTAG), Euclidean Nearest-Neighbor Distance distribution (ENN), Interspersion and Juxtaposition Index (IJI), Landscape Shape Index (LSI), Effective Mesh Size (MESH), Percentage of Like Adjacencies (PLADJ), Proximity Index distribution (PROX) and Splitting Index (SPLIT) (Fragstats 4.2 software user manual (McGarigal et al., 2012)).

Some of these variables' statistical distributions were summarized by their mean (MN), median (MD), area weighted mean (AM), standard deviation (SD), coefficient of variation (CV) and range (RA) (see table 3).

This analysis was performed by PSU (1×1km units) and employed land use/cover data from the *'COS 2012'* map in raster format (with a spatial resolution of 20m). All landscape metrics were calculated using Fragstats 4.2 software (McGarigal et al., 2012).

All the predictors previously described were (posteriorly) divided in five different groups, according to the hypothesis they were associated with (chapter 2.6.1.). This division and a summary of all variables are illustrated in table 4.

## 2.6. Data Analysis

### 2.6.1. Tested hypotheses

In order to meet the objectives of this study, an *a priori* defined set of hypotheses was developed based on scientific knowledge, relevant bibliographic references and expert-knowledge (supported by field observations) regarding factors influencing the distribution of passerine species richness.

These hypotheses are defined in Table 3 and Table 4 shows the predictive variables associated to each hypothesis.

Table 3 – Description of the set of hypotheses tested (H1 - H5) that could explain passerine species richness and references that support this determination.

| **Hypothesis** | | **Description** | **References** |
|---|---|---|---|
| **H1** | Climate and topography | Abiotic factors, related to climate and topography, are the main influencing factors determining passerine species richness | Correia et al., 2015; Evans et al., 2005b; Hawkins et al., 2003 |
| **H2** | Habitat diversity | Habitat diversity related to land cover/vegetation heterogeneity and the presence of multiple and/or diverse habitats and/or plant species in the study area is the main influencing factor determining passerine species richness | Joaquín Hortal et al., 2009; Schouten et al., 2009 |
| **H3** | Habitat disturbance | Habitat disturbance (*e.g.* land cover change and fire) is the main influencing factor determining passerine species richness | Falcucci et al., 2007; Lindenmayer et al., 2014 |
| **H4** | Landscape composition | Landscape composition related to the coverage of certain land cover and/or habitat types present in the study area (*e.g.* crops, bare rock, natural forest) is the main influencing factor determining passerine species richness | Haslem and Bennett, 2008; Wretenberg et al., 2010 |
| **H5** | Landscape structure | The spatial configuration of the landscape linked to patch area, patch edges, aggregation, shape and core area are the main influencing factor determining passerine species richness | Carrara et al., 2015; Schindler et al., 2013 |

Table 4 – Code name, description and respective hypothesis group of the predictive variables used in the modelling framework

| Hypothesis group | Code name | Variables Description | |
|---|---|---|---|
| H1 - Climate & Topography | BIO_02 | Mean diurnal range (Mean of monthly (max temp - min temp)) (ºC) | |
| | BIO_04 | Temperature seasonality (Standard deviation*100) (ºC) | |
| | BIO_05 | Max temperature of warmest month (ºC) | |
| | BIO_06 | Min temperature of coldest month (ºC) | |
| | BIO_15 | Precipitation seasonality (coefficient of variation) (mm) | |
| | BIO_16 | Precipitation of wettest quarter (mm) | |
| | BIO_17 | Precipitation of driest quarter (mm) | |
| | Elev_MN | Elevation (mean) (m) | |
| | Elev_SD | Elevation (standard deviation) (m) | |
| | Slope_MN | Slope; mean value for the 1km2 square (%) | |
| | Slope_SD | Slope (standard deviation) | |
| H2 - Habitat diversity | h_habitats | Shannon index of habitat types | |
| | hab_richness | Habitat richness | |
| | sp_richplant | Plant species richness | |
| H3 - Habitat disturbance | COS90_12_Cat_Change | Cover of areas that changed the land cover/use category between 1990-2012 | |
| | BurntPercMN_90_12 | Average 1990 - 2012 burnt area percentage (%) | |
| | BurntPercMN_03_12 | Average 2003 - 2012 burnt area percentage (%) | |
| | BurntPercMN_08_12 | Average 2008 - 2012 burnt area percentage (%) | |
| H4 - Landscape composition | annual_crops | Cover of annual crops (%) | |
| | bare_rock | Cover of bare rock areas (%) | |
| | built_up_areas | Cover of built up areas (%) | |
| | natural_forest | Cover of natural forest (%) | |
| | permanent_crops | Cover of permanent crops (%) | |
| | production_forest | Cover of production forest (%) | |
| | scrub_and_sparsely_vegetated | Cover of scrub and sparsely vegetated areas (%) | |
| H5 - Landscape structure | AREA* | Area and edge metrics | Patch Area Distribution |
| | ED | | Edge Density |
| | GYRATE* | | Radius of Gyration Distribution |
| | LPI | | Largest Patch Index |
| | TE | | Total Edge |
| | CIRCLE* | Shape metrics | Related Circumscribing Circle |
| | CONTIG* | | Contiguity Index |
| | FRAC* | | Fractal Index |
| | PAFRAC | | Perimeter-Area Fractal Dimension |
| | PARA* | | Perimeter-Area Ratio |
| | SHAPE* | | Shape Index |
| | CAI* | Core area metrics | Core Area Index |
| | CORE* | | Core Area |
| | DCAD | | Disjunct Core Area Density |
| | DCORE* | | Disjunct Core Area |
| | NDCA | | Number of Disjunct Core Areas |
| | TCA | | Total Core Area |
| | COHESION | Aggregation metrics | Patch Cohesion Index |
| | CONTAG | | Contagion Index |
| | DIVISION | | Landscape Division Index |
| | ENN* | | Euclidean Nearest Neighbor Distance |
| | IJI | | Interspersion & Juxtaposition Index |
| | LSI | | Landscape Shape Index |
| | MESH | | Effective Mesh Size |
| | NP | | Number of patches |
| | PD | | Patch Density |
| | PLADJ | | Percentage of Like Adjacencies |
| | PROX* | | Proximity Index |
| | SPLIT | | Splitting Index |

* The statistical distribution of this variable was summarized by mean (MN), median (MD), area-weighted mean (AM), standard deviation (SD), coefficient of variation (CV) and range (RA).

### 2.6.2. Modelling framework

To obtain a quantitative measure of the strength of evidence or support for each hypothesis, we created a representative multiple regression model for each one using its related variables and ranked them from best to least fit using a Multi-model Inference framework (MMI; Burnham and Anderson, 2002) based on Akaike Information Criterion (AIC). Model ranking and selection based on MMI and AIC provides a robust framework for statistical inference and is commonly used in ecological studies (*e.g.* Carrara et al., 2015; Correia et al., 2015; Mühlner et al., 2010). Using a 1:1 ratio of the hypotheses with their models allowed us to consider each hypothesis and its model as synonymous (Burnham et al., 2011). This modelling framework was composed by 5 steps (illustrated in Figure 5) and was applied to all the response variables, using the observed and estimated values of passerine species richness (separately). All analyses were performed in R statistical modelling software (version 3.1.3; Development Core Team, 2012).

#### Step 1 – Generating variable combinations

Given the high number of predictive variables associated with each hypothesis and the relatively low number of samples (n=24), we generated regression models with all possible combinations of predictive variables belonging to the same group, according to its hypothesis, using combinatorial functions from the *caTools* package in R (Tuszynski, 2008). These combinations included: univariate (one variable), bivariate (two variables) and multivariate models (with three variables maximum), thus avoiding some overfitting problems in relation to the small sample size. Additionally, this procedure allowed to explore potentially unnoticed associations between response and predictor variables and to maximize model performance by improving the selection of predictors for each response variable and hypothesis. Exceptionally, due to its high number of variables that would generate a large number of possible combinations, variables associated with hypothesis five (H5 – “Landscape structure”) were previously tested for correlation with the response variables. Using the Spearman’s rank correlation (r) test, we calculated the pair-wise correlations in order to minimize the number of predictors. This non-parametric test is commonly used to measure the degree of association between two variables without assuming a particular distribution (Borradaile, 2013). The predictors that correlated with the response variables up to a threshold equal of $r \geq |0.3|$ were selected for further analysis.

To improve variable selection by diminishing multicollinearity issues and reduce processing time, we calculated the square root of the Variance Inflation Factors (VIF) for each combination. VIF is a statistic used to measure possible multicollinearity amongst the predictor variables of regression models, which can increase estimates of parameter variance (Robinson and Schumacker, 2009), *i.e.*, VIF reports how much of the predictors' variability is explained by the rest of the predictors in the model due to correlation among those predictors (Craney and Surles, 2002). If models presented any $\sqrt{VIF} \geq 2$ they were excluded; those with any $\sqrt{VIF} < 2$ were used in the next step. For this calculation, we used Generalized Linear Models (GLM) and specified the family as Poisson (commonly used for count data such as species richness; Guisan et al., 2002).

**Step 2 – Generating GAM models**

The models selected in the previous step were transformed into Generalized Additive Models (GAM; with a smoothing factor equal to 2, additionally controlling some overfitting problems) and calibrated using the *mgcv* package in R (Wood, 2011). GAM models are flexible statistical methods that take into account the interactive behavior of the variables (whose effects are commonly not linear), which is commonly overlooked in Generalized Linear Models (Elith and Leathwick, 2009; Guisan et al., 2002; Leathwick et al., 2006; Meynard and Quinn, 2007).

**Step 3 – Ranking the hypothesis' models**

All GAM models generated in the previous step were ranked according to the Akaike's Information Criterion with a correction for small sample sizes (AICc) (Burnham and Anderson, 2002; Symonds and Moussalli, 2010) using the R function "AICctab" from the *bbmle* package (Bolker, 2010). This information criterion attributes a numerical value by which competing models are ranked regarding information loss in approximating full reality (Symonds and Moussalli, 2011), allowing their evaluation rather than only comparing two models as in inferential statistics (Burnham et al., 2011).

In this step we calculated the AICc and ΔAIC values and Akaike weights of each model. The AICc value provides a relative measure, deriving meaning from the comparison with the AICc values of the other models tested. The model with the lowest AICc value was identified as the best model (Burnham and Anderson, 2002) for that hypothesis, due to its highest explanatory power and support. ΔAICc values provide a measure of the loss of information between a given model of the set and the best model, i.e. the strength of support for the model decreases with the increase of ΔAICc values. Models with $\Delta AICc<2$ are considered to have the best support to explain the data.

However, models with ΔAICc ranging between 2-7 should not be dismissed since they still have some support, which greatly decreases from models with ΔAICc > 9 (Burnham et al., 2011). Akaike weights, being the probability that a model is the best of the set, varies between 0 and 1.

**Step 4 – Selecting the top 5 models**

This step consisted of a *first selection phase,* following the ranking of model combinations for a given hypothesis, and was responsible for selecting the single 'best model' to represent that hypothesis, *i.e.*, the model with lowest AICc. Iteratively, the steps 1 to 4 were repeated for each hypothesis from H1 to H5, thus maintaining the same selection criteria. All the selected models and related predictors are presented in appendix II.

**Step 5 – Final ranking and selection of the top 5 models**

This step consisted of a *second selection phase*. After selecting the five best models (one for each hypothesis) we added a '*Null hypothesis*' (hereafter termed H0) to the model set and ranked it using the same model ranking and selection procedure based on information-theoretic measures (AICc) to that applied in steps 3 and 4. The null hypothesis consisted in a model without any predictive variable and including a single intercept term. This allows a relative evaluation of the models through the comparison between the null hypothesis' model and the other hypotheses' models. If H0 was included in the confidence set (i.e., the set of models with highest support: ΔAIC<2) this was considered indicative that the models do not have a good performance or support.

Complementarily to MMI measures we also calculated a set of measures of goodness-of-fit and model performance, namely: Deviance ($D^2$), Adjusted Deviance ($adjD^2$) and the Spearman correlation (corSp) between predicted and observed values (Burnham et al., 2011).

To further explore the relationship between response variables and selected predictive variables (selected in step 4), smooth response curves were generated by univariate GAM models and the Spearman correlation was also calculated as a general measure of association.

### 2.6.3. Defining aggregate sets of variables based on their responses to environmental factors

Using Akaike weights it was possible to define the relative contribution of each hypothesis (encompassing a group of environmental factors, *e.g.* landscape composition or configuration, disturbance, climate) to explain the distribution of passerine species richness as a whole or by species traits. Using this data and a cluster analysis algorithm, we obtained groups of variables with similar responses to environmental drivers. After applying the modeling framework, hierarchical cluster analysis (HCA) was performed with a Euclidean distance matrix based on Akaike weights obtained from the multi-model inference (MMI) analysis in step 5 (Appendix III, a).

For comparison effects, we also performed HCA using a distance matrix based on: 1 – Spearman Correlation between the response variables. This allowed to compare dendrograms' structure: one based on the responses to environmental factors and, the other based solely on the redundancy and co-occurrence patterns of total species and/or species richness by feeding or habitat traits (Appendix III, b). In both cases, HCA used the Ward D2 method (Murtagh and Legendre, 2014) as the clustering criterion implemented in the *hclust* R function.

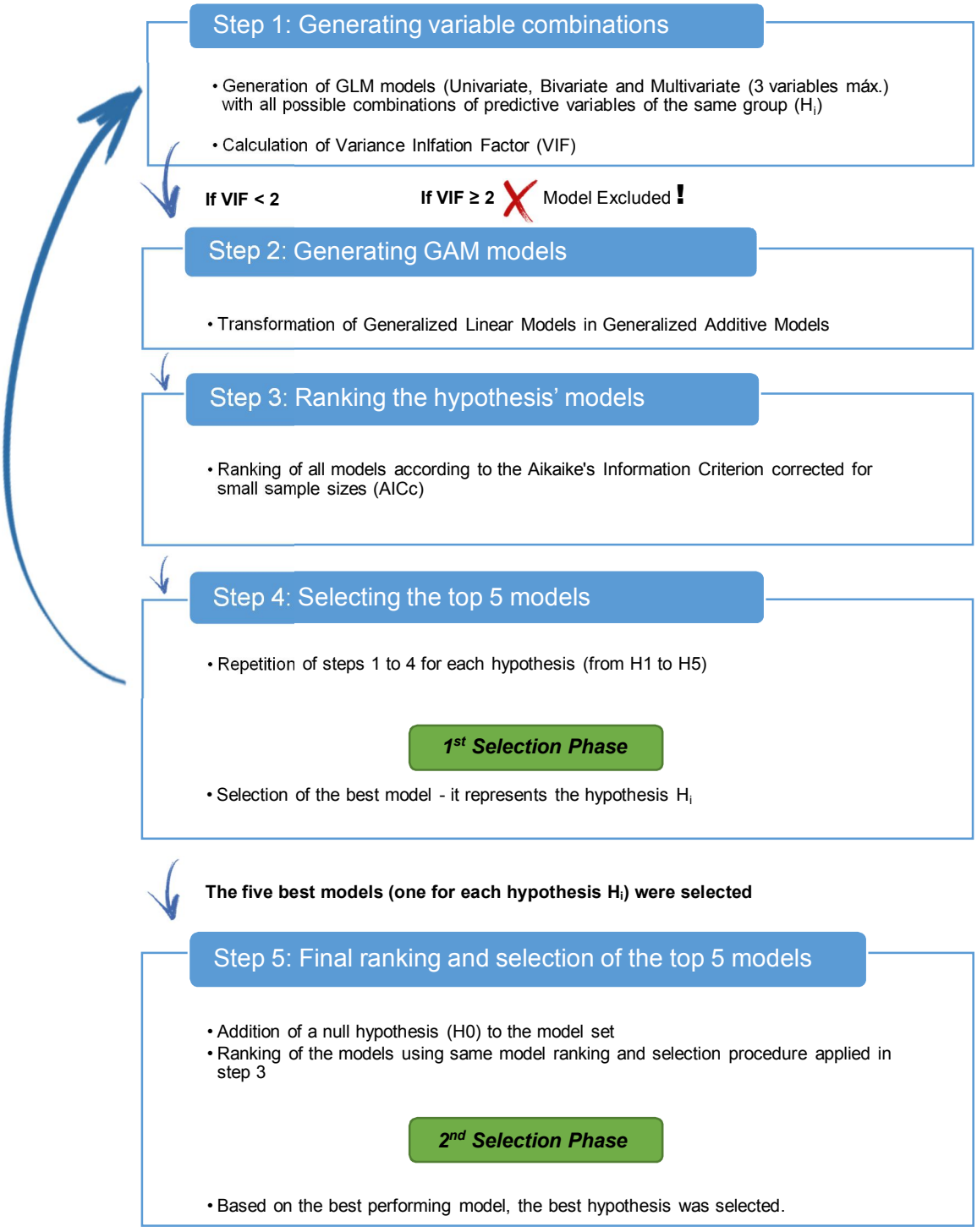


Figure 5 – Modelling framework, based on Multi-model Inference, applied to each response variable (observed and estimated) in order to obtain a quantitative measure of the strength of evidence for each hypothesis.

# 3. Results

## 3.1. Overall bird species richness and diversity

Overall, 61 passerine species were recorded (Appendix IV), ranging from 9 to 26 per sampling unit (Appendix V). These species belonged to 21 different families (ranging from 7 to 12 per plot; see Figure 6) and, according to its feeding habits, 12 were omnivorous, 36 were insectivorous and 13 were granivorous. Regarding its foraging habitat, 12 of the recorded species were shrubland specialists, 20 were woodland specialists and 29 were open area specialists.

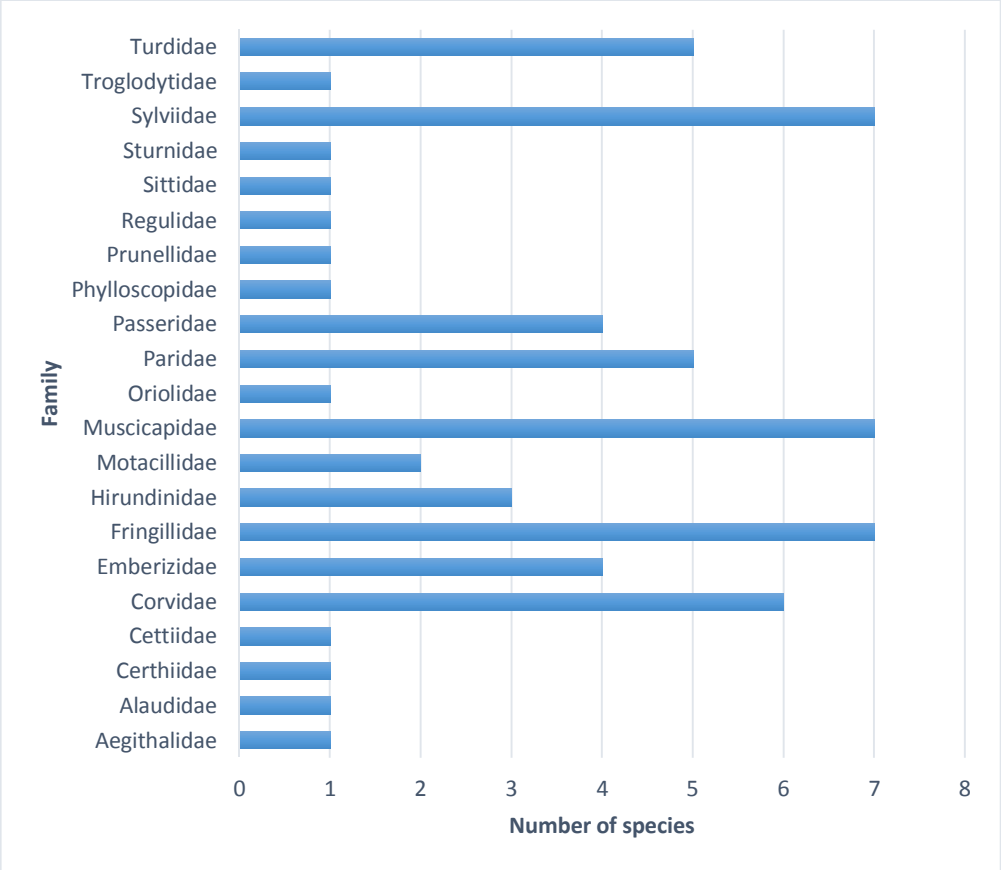


Figure 6 – Number of passerine species by family recorded the Vez watershed during May/June 2014.

In turn, SAR modelling (Figure 7) estimated an average of 31 passerine species, ranging from 12 to 51 per PSU (Appendix V). Regarding its feeding habits, this method estimated the presence of (on average, per PSU) 21 insectivorous species, 3 omnivorous species and 10 granivorous. As regards its foraging habitat, it estimated, on average, 15 open area specialist species, 5 shrub specialist species and 14 woodland specialist species.

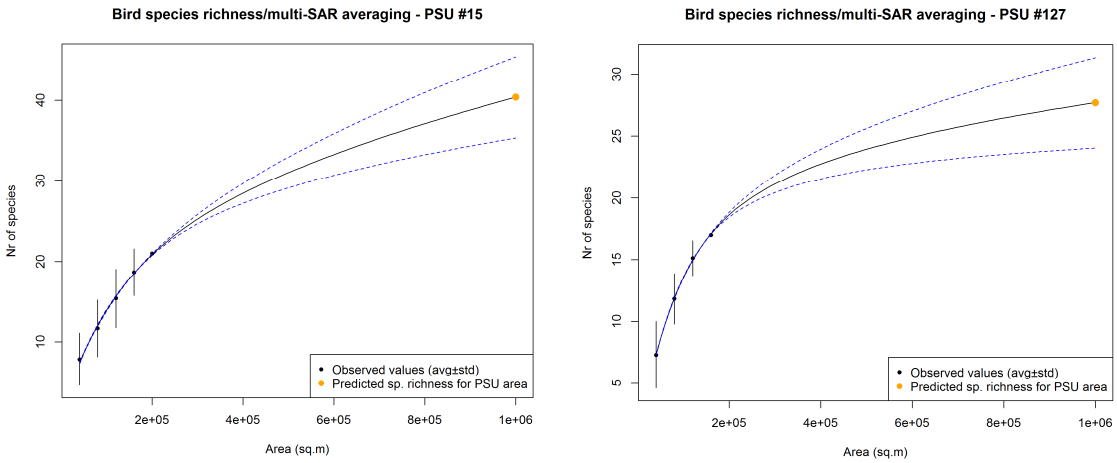


Figure 7 – Species-Area relationship curve graphic used to estimate passerine species richness in Primary Sampling Unit number 15 (PSU#15) and number 127 (PSU #127).

The overall distribution of SAR-estimated passerine species richness originated, as expected, highly superior values relatively to observed ones. This distribution is graphically illustrated in Figure 8 and summarized on the Appendix V.

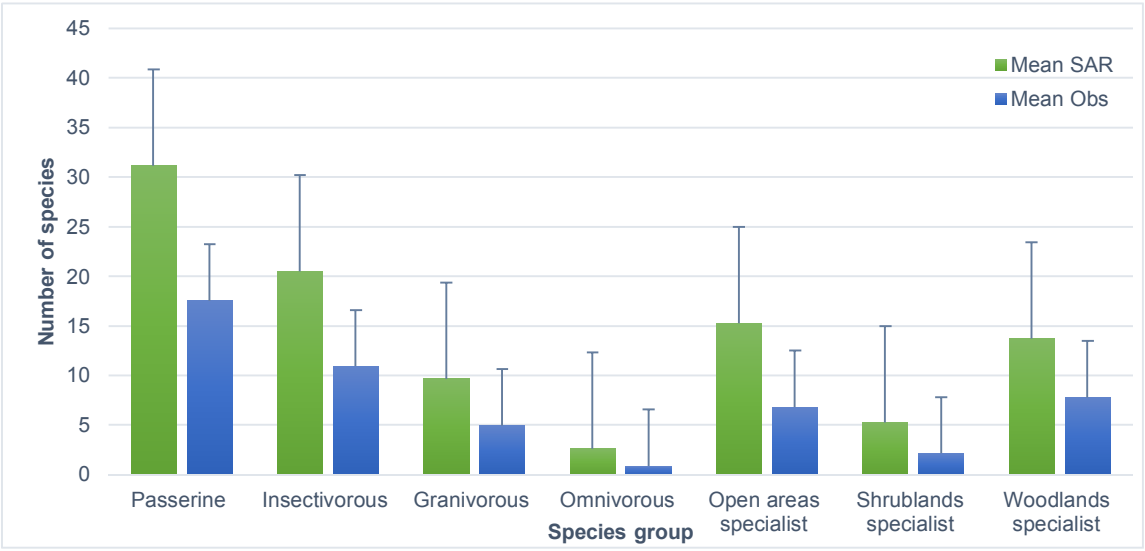


Figure 8 – Mean observed (Obs) and estimated (SAR) passerine species richness distribution in the Vez watershed during May/June 2014. Vertical bars represent standard deviation.

### 3.2. Ranking of hypotheses

Overall, models using SAR-estimated values performed better than those based on observed values. They presented higher values of Spearman correlation and deviance and adjusted deviance values were significantly superior (Figure 9). Considering this, subsequent results based on SAR-estimated values were highlighted and given more relevance.

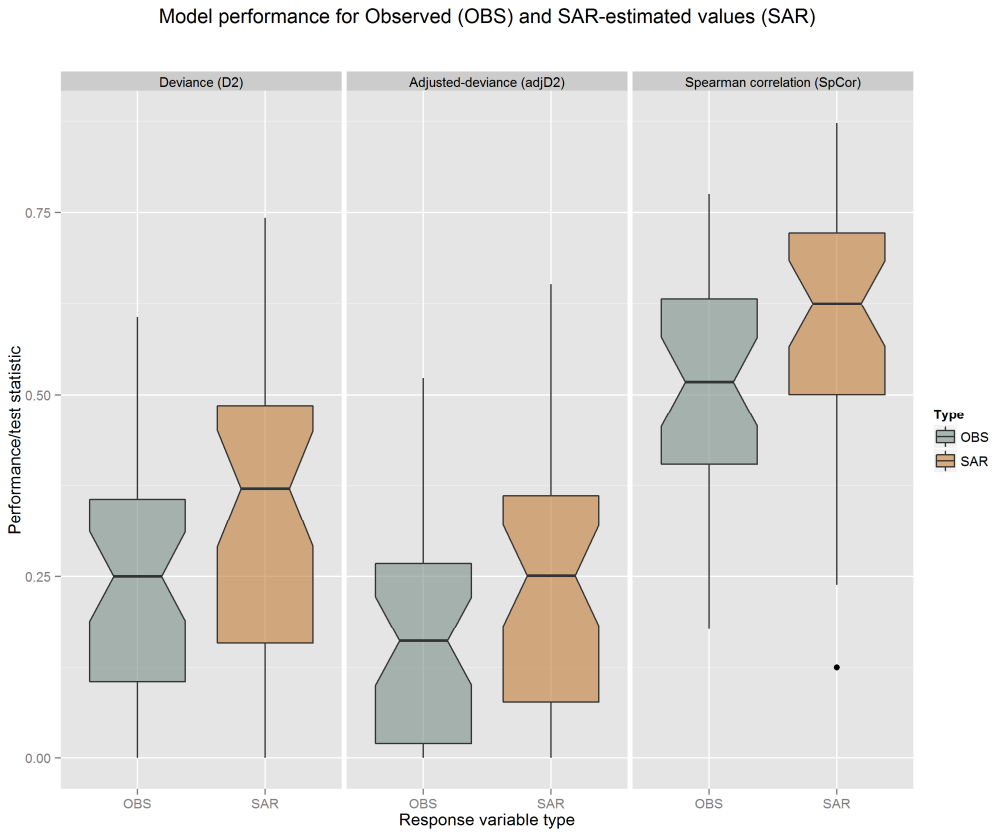


Figure 9 – Boxplots showing the distribution of model performance values based on Observed (OBS) and SAR-estimated (SAR) response variables, according to Deviance ($D^2$), Adjusted-deviance ($adjD^2$) and Spearman correlation (SpCor) values.

#### 3.2.1. Total Passerine Species Richness

Generally, best performing models revealed good performance for explaining the distribution of passerine species richness (both observed and SAR-estimated), with corSp > 0.5. However, this measure was higher when using estimated values (corSp= 0.714 for H5 vs. corSp=0.588 for H2; Table 5). The same occurred with deviance ($D^2$)

and adjusted-deviance (adj$D^2$), with models based on estimated species richness presenting the highest values (0.605 and 0.465, respectively).

According to the results obtained from MMI (Table 5), the models H2 and H5 obtained the highest support for explaining observed passerine species richness (i.e., ΔAIC<2). However, their Akaike weights were fairly similar (w=0.40 and w=0.39, respectively) which indicates considerable model uncertainty.

Regarding the SAR-estimated values, model H5 was pointedly more successful explaining this response variable than others, with an Akaike weight equal to 0.92.

Table 5 - Results from Akaike's information criterion model ranking for bird species richness. Competing models are ordered from best to least fit hypothesis by the AICc values. Models with ΔAIC < 2 are highlighted.

| Estimated values (SAR) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Hypothesis** | **AICc** | **ΔAICc** | **Df** | **wi** | **corSp** | **$D^2$** | **adj$D^2$** |
| H5 | Landscape structure | 162.25 | 0.00 | 5.7 | 0.92 | 0.714 | 0.605 | 0.465 |
| H4 | Landscape composition | 168.12 | 5.88 | 4.7 | 0.05 | 0.625 | 0.475 | 0.365 |
| H2 | Habitat diversity | 169.12 | 6.87 | 2.8 | 0.03 | 0.587 | 0.395 | 0.338 |
| H1 | Climate & Topography | 172.59 | 10.35 | 4.9 | 0.01 | 0.685 | 0.409 | 0.200 |
| H3 | Habitat disturbance | 175.62 | 13.37 | 2.7 | 0.00 | 0.509 | 0.287 | 0.219 |
| H0 | Null hypothesis | 189.97 | 27.72 | 1.0 | 0.00 | − | 0.000 | 0.000 |
| Observed values | | | | | | | | |
| | **Hypothesis** | **AICc** | **ΔAICc** | **Df** | **wi** | **corSp** | **$D^2$** | **adj$D^2$** |
| H2 | Habitat diversity | 135.04 | 0.00 | 2.0 | 0.40 | 0.588 | 0.323 | 0.258 |
| H5 | Landscape structure | 135.10 | 0.06 | 2.5 | 0.39 | 0.602 | 0.360 | 0.299 |
| H1 | Climate & Topography | 138.20 | 3.16 | 3.4 | 0.08 | 0.544 | 0.316 | 0.172 |
| H3 | Habitat disturbance | 138.59 | 3.55 | 2.4 | 0.07 | 0.438 | 0.220 | 0.146 |
| H4 | Landscape composition | 139.36 | 4.32 | 3.1 | 0.05 | 0.520 | 0.250 | 0.092 |
| H0 | Null hypothesis | 141.87 | 6.83 | 1.0 | 0.01 | − | 0.000 | 0.000 |

This model (H5) was composed of the variables MESH (Effective Mesh Size; figure 10, A; Appendix VI), PROX_CV (Coefficient of variation of Proximity Index; figure 10, B; Appendix VI) and CONTIG_SD (Standard Deviation of Contiguity Index; figure 10, C; Appendix VI). MESH, showed a nonlinear relationship with total passerine species richness (with some potential outlier effects at the right-tail of the distribution), and was negatively correlated with it, contrary to the other two predictor variables, which were both positively correlated. Despite this fact and the linear relationship shared, the correlation between CONTIG_SD and passerine species richness was low (SpCor=0.36). In turn, PROX_CV was highly correlated with this response variable (SpCor=0.61), almost presenting a linear relationship.

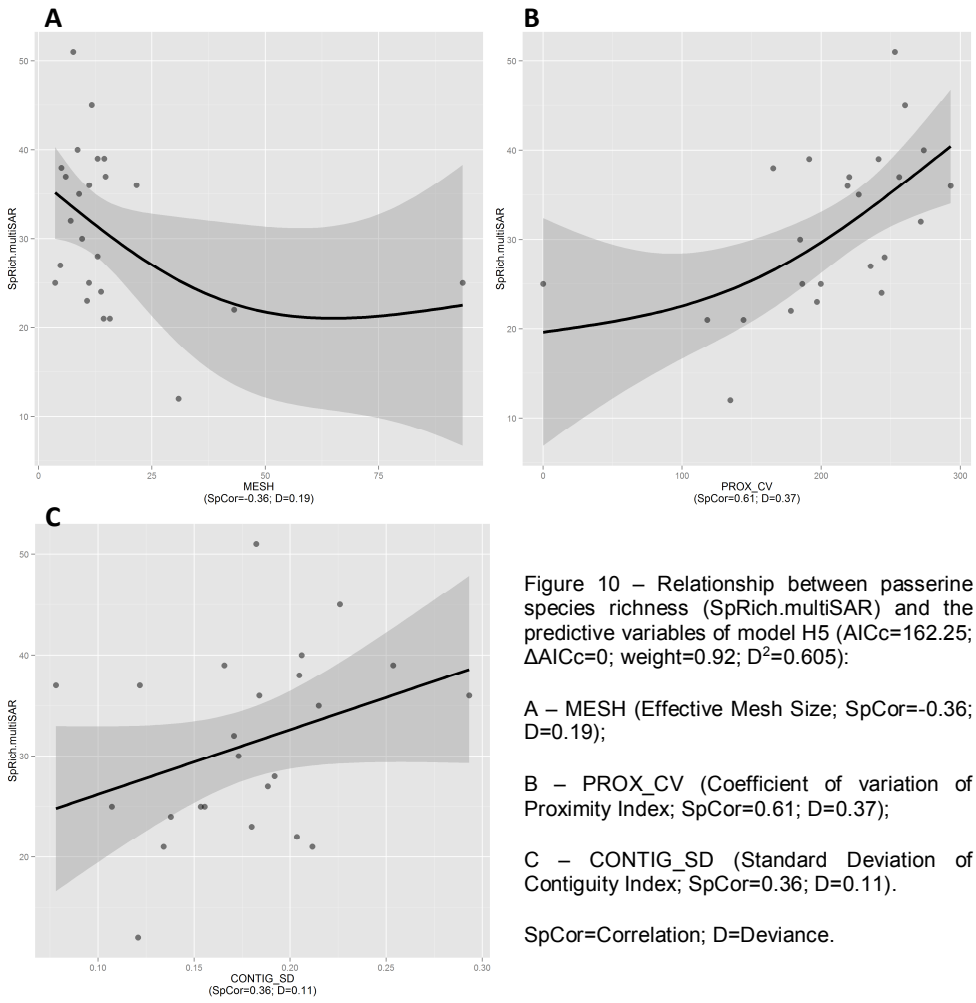


Figure 10 – Relationship between passerine species richness (SpRich.multiSAR) and the predictive variables of model H5 (AICc=162.25; ΔAICc=0; weight=0.92; $D^2$=0.605):

A – MESH (Effective Mesh Size; SpCor=-0.36; D=0.19);

B – PROX_CV (Coefficient of variation of Proximity Index; SpCor=0.61; D=0.37);

C – CONTIG_SD (Standard Deviation of Contiguity Index; SpCor=0.36; D=0.11).

SpCor=Correlation; D=Deviance.

### 3.2.2. Passerine species richness by feeding habit

#### *Number of Insectivorous species*

All the best models revealed good performance to explain SAR-estimated insectivorous species richness, with corSp > 0.7. However, this correlation was lower for observed values, varying between 0.4 and 0.6 (Table 6). Similarly, deviance ($D^2$) and adjusted deviance (adj$D^2$) declined from estimated to observed species richness, with the latter presenting the lowest values of 0.185 and 0.108, respectively.

The most successful models for explaining the observed number of insectivorous species were H5, H2, H1 and H4, with similar Akaike weights (w=0.33, w=0.20, w=0.19, w=0.16, respectively; see Table 6).

Models based on estimated values disclosed higher explanatory success for hypotheses H4 and H2, with higher Akaike weights equal to 0.47 and 0.38, respectively.

Table 6 – Results from Akaike's information criterion model ranking for number of insectivorous bird species. Competing models are ordered from best to least fit hypothesis by the AICc values. Models with ΔAIC < 2 are highlighted.

| Estimated values (SAR) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Hypothesis** | **AICc** | **ΔAICc** | **df** | **wi** | **corSp** | **$D^2$** | **adj$D^2$** |
| H4 | Landscape composition | 149.17 | 0.00 | 3.9 | 0.47 | 0.748 | 0.422 | 0.301 |
| H2 | Habitat diversity | 149.58 | 0.42 | 2.5 | 0.38 | 0.659 | 0.349 | 0.287 |
| H5 | Landscape structure | 152.47 | 3.30 | 2.0 | 0.09 | 0.523 | 0.258 | 0.188 |
| H3 | Habitat disturbance | 154.72 | 5.55 | 3.9 | 0.03 | 0.410 | 0.298 | 0.150 |
| H1 | Climate & Topography | 154.96 | 5.79 | 4.8 | 0.03 | 0.761 | 0.333 | 0.097 |
| H0 | Null hypothesis | 161.81 | 12.64 | 1.0 | 0.00 | − | 0.000 | 0.000 |
| Observed values | | | | | | | | |
| | **Hypothesis** | **AICc** | **ΔAICc** | **df** | **wi** | **corSp** | **$D^2$** | **adj$D^2$** |
| H5 | Landscape structure | 120.05 | 0.00 | 2.0 | 0.33 | 0.604 | 0.259 | 0.189 |
| H2 | Habitat diversity | 121.01 | 0.95 | 2.1 | 0.20 | 0.460 | 0.224 | 0.151 |
| H1 | Climate & Topography | 121.11 | 1.05 | 2.7 | 0.19 | 0.518 | 0.277 | 0.208 |
| H4 | Landscape composition | 121.49 | 1.44 | 2.0 | 0.16 | 0.382 | 0.185 | 0.108 |
| H0 | Null hypothesis | 123.19 | 3.13 | 1.0 | 0.07 | − | 0.000 | 0.000 |
| H3 | Habitat disturbance | 123.93 | 3.88 | 2.3 | 0.05 | 0.336 | 0.097 | 0.011 |

Model H2 included a single predictor (h_habitats – Shannon Index of Habitat types), and presented a positive nonlinear relationship and high correlation (SpCor=0.66) with insectivorous species richness (figure 11, A). In turn, its relationship with variables natural_forest (Percentage cover of natural forest) and production_forest (Percentage cover of production forest), which consist on the bivariate model H4, were linear (figure 11, B) and nonlinear (figure 11, C), respectively. The former was also positively correlated (SpCor= 0.55), showing that even low percentages (<30%) of natural forest have a boosting effect on the richness for this species group. Similarly, production forest has a positive relationship with insectivorous species richness when in small percentages (<20%); however, when this percentage increases above this limit, the relationship becomes negative.

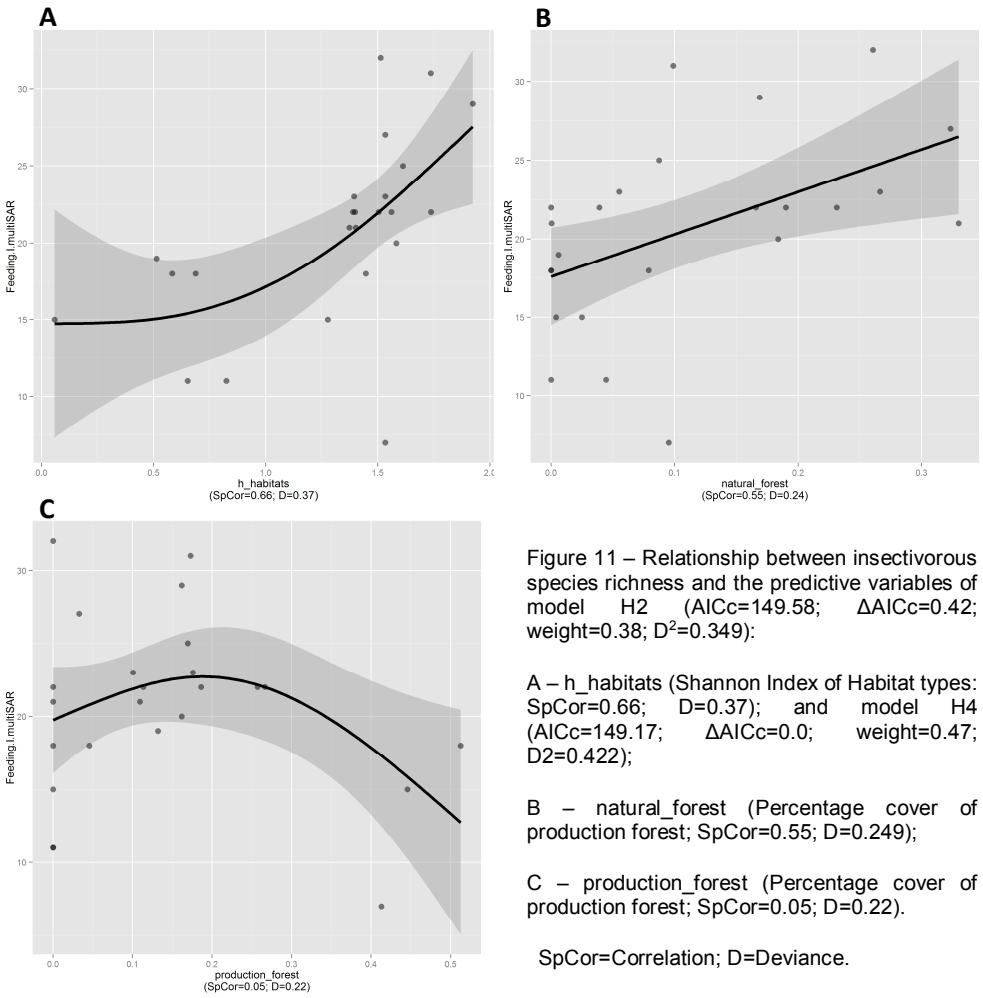


Figure 11 – Relationship between insectivorous species richness and the predictive variables of model H2 (AICc=149.58; ΔAICc=0.42; weight=0.38; $D^2$=0.349):

A – h_habitats (Shannon Index of Habitat types: SpCor=0.66; D=0.37); and model H4 (AICc=149.17; ΔAICc=0.0; weight=0.47; D2=0.422);

B – natural_forest (Percentage cover of production forest; SpCor=0.55; D=0.249);

C – production_forest (Percentage cover of production forest; SpCor=0.05; D=0.22).

SpCor=Correlation; D=Deviance.

### *Number of Granivorous species*

All the best performing models revealed with a good performance to explain SAR-estimated granivorous species richness, with corSp > 0.7; however, this value decreased for observed species richness, varying between 0.3 and 0.5 (Table 7). Similarly, deviance ($D^2$) and adjusted deviance ($adjD^2$) declined from estimated to observed species richness, with the former presenting higher values ($D^2$>0.7 and $adjD^2$>0.6) relatively to the latter's values, which were relatively low ($D^2$ < 0.3 and $adjD^2$< 0.2).

Considering the observed number of granivorous species, all hypotheses (with the exception of H4), obtained substantial support (ΔAICc<2; see table 7), with H5 and H4 having the higher Akaike weights (w=0.31 and w=0.20, respectively). The models' low Akaike weights and the inclusion of H0 (null hypothesis) in the confidence set (ΔAIC<2) revealed a high uncertainty.

The models' relatively low Akaike weights and the inclusion of H0 ('Null hypothesis') in the confidence set (ΔAIC<2) revealed a high uncertainty.

In contrast, when considering models using SAR estimated values, models H5 and H3 stood out from the rest, their closest model (based on AICc values) having ΔAIC=14.55. Model H5, which had the best performance, had a high Akaike weight, equal to 0.67.

Table 7 - Results from Akaike's information criterion model ranking for number of granivorous bird species. Competing models are ordered from best to least fit hypothesis by the AICc values. Models with ΔAIC < 2 are highlighted.

| Estimated values (SAR) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Hypothesis** | **AICc** | **ΔAICc** | **df** | **$w_i$** | **corSp** | **$D^2$** | **adj$D^2$** |
| H5 | Landscape structure | 121.65 | 0.00 | 5.4 | 0.67 | 0.768 | 0.742 | 0.650 |
| H3 | Habitat disturbance | 123.04 | 1.40 | 3.9 | 0.33 | 0.654 | 0.656 | 0.584 |
| H1 | Climate & Topography | 136.20 | 14.55 | 3.0 | 0.00 | 0.549 | 0.382 | 0.252 |
| H4 | Landscape composition | 143.28 | 21.64 | 4.6 | 0.00 | 0.125 | 0.314 | 0.170 |
| H0 | Null hypothesis | 152.98 | 31.33 | 1.0 | 0.00 | − | 0.000 | 0.000 |
| H2 | Habitat diversity | 154.22 | 32.58 | 2.0 | 0.00 | 0.301 | 0.015 | 0.000 |
| Observed values | | | | | | | | |
| | **Hypothesis** | **AICc** | **ΔAICc** | **df** | **$w_i$** | **corSp** | **$D^2$** | **adj$D^2$** |
| H3 | Habitat disturbance | 97.54 | 0.00 | 2.0 | 0.31 | 0.516 | 0.250 | 0.179 |
| H5 | Landscape structure | 98.41 | 0.87 | 2.5 | 0.20 | 0.509 | 0.259 | 0.189 |
| H2 | Habitat diversity | 99.16 | 1.62 | 2.0 | 0.14 | 0.397 | 0.147 | 0.065 |
| H1 | Climate & Topography | 99.26 | 1.72 | 2.0 | 0.13 | 0.312 | 0.140 | 0.058 |
| H0 | Null hypothesis | 99.40 | 1.86 | 1.0 | 0.12 | − | 0.000 | 0.000 |
| H4 | Landscape composition | 99.83 | 2.29 | 2.0 | 0.10 | 0.178 | 0.103 | 0.018 |

Model H3 (bivariate) was composed of variables BurntPercMN_90_12 (Average 1990-2012 burnt area percentage) and COS90_12_Cat_Change (Cover areas that changed land cover/use category between 1990-2012). The former presented a negative relationship with granivorous species richness (figure 12, A). In this case, GAM response curve picked up a nonlinear behavior (with low correlation, SpCor=0.15) due to the presence of an outlier in the right-side of the distribution. In turn, COS90_12_Cat_Change was positively correlated (SpCor=0.59) with this groups' species richness (figure 12, B). Model H5 consisted of variables CONTIG_SD (Standard deviation of Contiguity Index), GYRATE_RA (Range of Radius of Gyration; Appendix VI) and SPLIT (Splitting Index, Appendix VI). GYRATE_RA (figure 12, D) and SPLIT (figure 12, E) displayed a linear relationship weakly correlated with the number of granivorous species (SpCor=-0.23 and 0.03, respectively). Finally, CONTIG_SD showed a nonlinear relationship, which is negative when the standard-deviation of Contiguity Index is relatively low (0.10 – 0.18), but turns positive when relatively low (0.10 – 0.18), but turns positive when CONTIG_SD increases (0.18 – 0.29; figure 12, C).

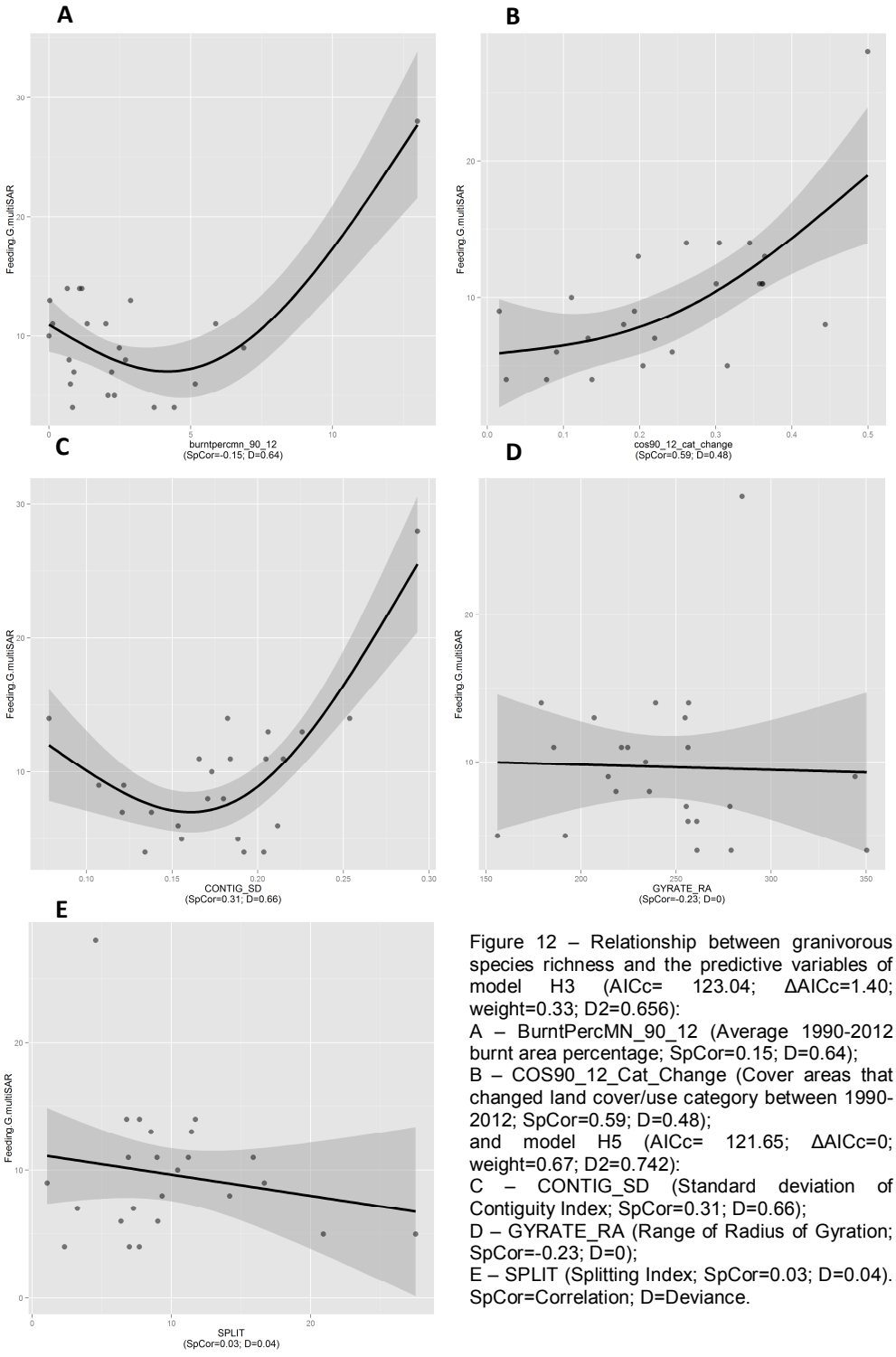


Figure 12 – Relationship between granivorous species richness and the predictive variables of model H3 (AICc= 123.04; ΔAICc=1.40; weight=0.33; D2=0.656):
A – BurntPercMN_90_12 (Average 1990-2012 burnt area percentage; SpCor=0.15; D=0.64);
B – COS90_12_Cat_Change (Cover areas that changed land cover/use category between 1990-2012; SpCor=0.59; D=0.48);
and model H5 (AICc= 121.65; ΔAICc=0; weight=0.67; D2=0.742):
C – CONTIG_SD (Standard deviation of Contiguity Index; SpCor=0.31; D=0.66);
D – GYRATE_RA (Range of Radius of Gyration; SpCor=-0.23; D=0);
E – SPLIT (Splitting Index; SpCor=0.03; D=0.04).
SpCor=Correlation; D=Deviance.

***Number of Omnivorous species***

All the best performing models revealed very good performance to explain omnivorous species richness (both observed and estimated), with corSp > 0.8. Likewise, both presented high deviance and adjusted deviance values, with $D^2$>0.6 and adj$D^2$>0.5 (Table 8).

Both models using observed or SAR-estimated values, the most successful hypothesis explaining the number of omnivorous species was H5 (Table 8). However, estimated values provided a higher Akaike weight of the model, with w=1.00 and ΔAIC's ranging from 0.00 to 44.77, comparatively to the observed values (w=0.67 and 0.00 < ΔAIC < 12.91).

Table 8 – Results from Akaike's information criterion model ranking for number of omnivorous bird species. Competing models are ordered from best to least fit hypothesis by the AICc values. Models with ΔAIC < 2 are highlighted.

| Estimated values (SAR) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Hypothesis** | **AICc** | **ΔAICc** | **df** | **$w_i$** | **corSp** | **$D^2$** | **adj$D^2$** |
| H5 | Landscape structure | 80.04 | 0.00 | 6.8 | 1.00 | 0.873 | 0.743 | 0.652 |
| H2 | Habitat diversity | 94.28 | 14.24 | 2.9 | 0.00 | 0.550 | 0.449 | 0.397 |
| H1 | Climate & Topography | 94.53 | 14.50 | 5.7 | 0.00 | 0.730 | 0.524 | 0.356 |
| H4 | Landscape composition | 96.42 | 16.38 | 5.4 | 0.00 | 0.671 | 0.490 | 0.310 |
| H3 | Habitat disturbance | 122.77 | 42.73 | 3.7 | 0.00 | 0.239 | 0.099 | 0.000 |
| H0 | Null hypothesis | 124.81 | 44.77 | 1.0 | 0.00 | − | 0.000 | 0.000 |
| Observed values | | | | | | | | |
| | **Hypothesis** | **AICc** | **ΔAICc** | **df** | **$w_i$** | **corSp** | **$D^2$** | **adj$D^2$** |
| H5 | Landscape structure | 49.66 | 0.00 | 3.0 | 0.67 | 0.762 | 0.606 | 0.523 |
| H1 | Climate & Topography | 52.44 | 2.78 | 3.0 | 0.17 | 0.718 | 0.507 | 0.403 |
| H2 | Habitat diversity | 53.19 | 3.54 | 2.8 | 0.11 | 0.560 | 0.468 | 0.417 |
| H4 | Landscape composition | 55.01 | 5.35 | 3.5 | 0.05 | 0.659 | 0.451 | 0.335 |
| H3 | Habitat disturbance | 62.24 | 12.59 | 2.0 | 0.00 | 0.233 | 0.084 | 0.000 |
| H0 | Null hypothesis | 62.56 | 12.91 | 1.0 | 0.00 | − | 0.000 | 0.000 |

Model H5 was a multivariate model including three variables: CORE_AM (Area-weighted mean of Core area; Appendix VI), PARA_RA (Range of Perimeter-Area ratio; Appendix VI) and CONTIG_SD (Standard deviation of Contiguity Index). PARA_RA (figure 13, B) and CONTIG_SD (figure 13, C) related negatively and positively with omnivorous species richness, correspondingly, but were very weakly correlated (SpCor= -0.05 and 0.02). However, CORE_AM (figure 13, A) had a higher correlation (SpCor=-0.51), exhibiting a nonlinear negative relationship with this group species (partially driven by a positive outlier in the right-side of the distribution).

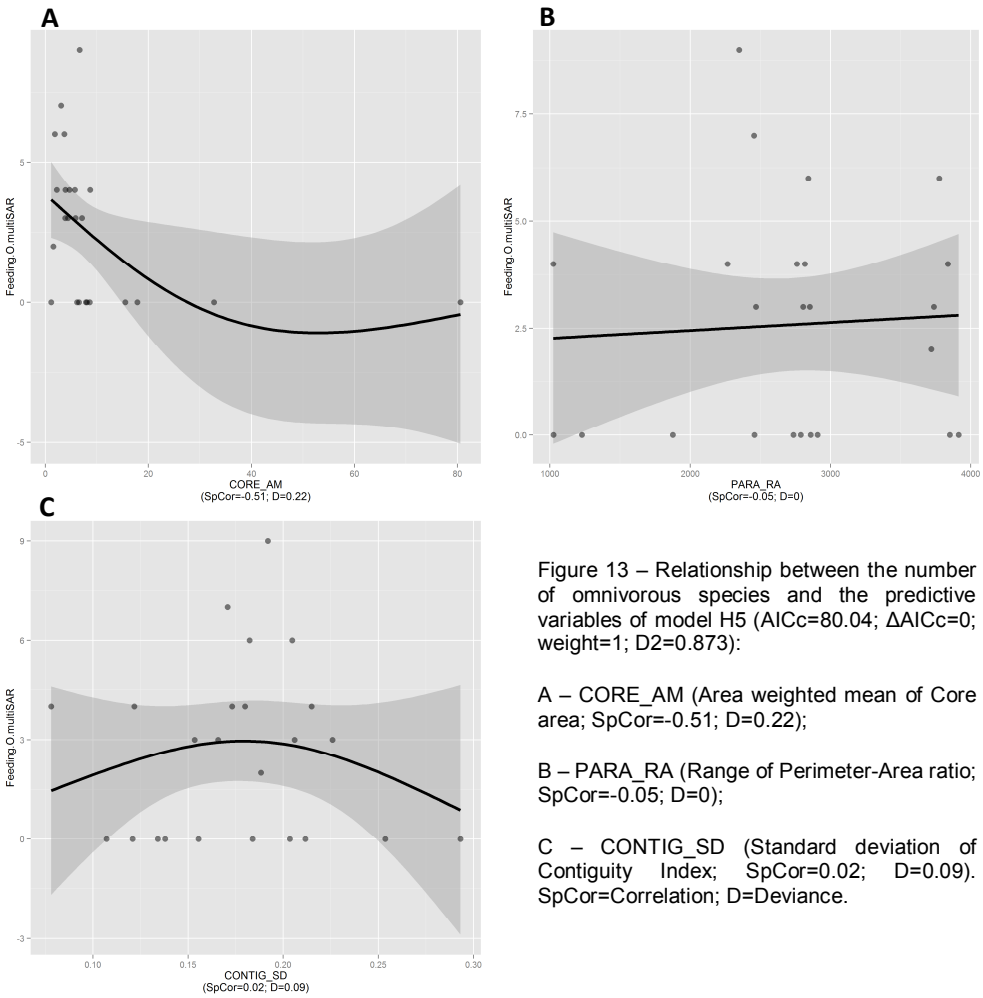


Figure 13 – Relationship between the number of omnivorous species and the predictive variables of model H5 (AICc=80.04; ΔAICc=0; weight=1; D2=0.873):

A – CORE_AM (Area weighted mean of Core area; SpCor=-0.51; D=0.22);

B – PARA_RA (Range of Perimeter-Area ratio; SpCor=-0.05; D=0);

C – CONTIG_SD (Standard deviation of Contiguity Index; SpCor=0.02; D=0.09). SpCor=Correlation; D=Deviance.

### 3.2.3. Passerine species richness by foraging habitat

#### *Number of Open areas specialist species*

All the best performing models revealed with a good performance to SAR-estimated open area specialist species richness, with corSp > 0.7 and low performance for observed species richness, varying between 0.2 and 0.4 (Table 9). Similarly, deviance ($D^2$) and adjusted deviance ($adjD^2$) declined from estimated to observed species richness, with the former presenting higher values ($D^2$=0.618 and $adjD^2$=0.483) relatively to the latter's values ($D^2$ < 0.4 and $adjD^2$< 0.2).

Hypotheses H4, H5, H1 and H2 were the most successful explaining the observed number of passerine species that are specialist of open areas with similar Akaike weights (Table 9) with model H4 attaining the highest Akaike weight (w=0.30), closely followed

by model H5 (w=0.28). MMI results for SAR-estimated values revealed a substantial support for model H5 (w=1.00).

Table 9 - Results from Akaike's information criterion model ranking for number of bird species that inhabit open areas. Competing models are ordered from best to least fit hypothesis by the AICc values. Models with ΔAIC < 2 are highlighted.

| Estimated values (SAR) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Hypothesis** | **AICc** | **ΔAICc** | **df** | **$w_i$** | **corSp** | **$D^2$** | **adj$D^2$** |
| H5 | Landscape structure | 146.92 | 0.00 | 6.2 | 1.00 | 0.791 | 0.618 | 0.483 |
| H4 | Landscape composition | 160.24 | 13.32 | 4.8 | 0.00 | 0.587 | 0.383 | 0.253 |
| H1 | Climate & Topography | 160.29 | 13.36 | 4.9 | 0.00 | 0.670 | 0.385 | 0.255 |
| H2 | Habitat diversity | 164.90 | 17.98 | 2.6 | 0.00 | 0.399 | 0.248 | 0.177 |
| H3 | Habitat disturbance | 171.83 | 24.91 | 2.8 | 0.00 | 0.358 | 0.157 | 0.076 |
| H0 | Null hypothesis | 178.95 | 32.03 | 1.0 | 0.00 | − | 0.000 | 0.000 |
| Observed values | | | | | | | | |
| | **Hypothesis** | **AICc** | **ΔAICc** | **df** | **$w_i$** | **corSp** | **$D^2$** | **adj$D^2$** |
| H4 | Landscape composition | 114.27 | 0.00 | 3.6 | 0.30 | 0.732 | 0.362 | 0.228 |
| H5 | Landscape structure | 114.39 | 0.12 | 2.8 | 0.28 | 0.467 | 0.300 | 0.233 |
| H1 | Climate & Topography | 114.81 | 0.54 | 2.0 | 0.23 | 0.411 | 0.226 | 0.152 |
| H2 | Habitat diversity | 115.64 | 1.36 | 2.0 | 0.15 | 0.412 | 0.197 | 0.120 |
| H0 | Null hypothesis | 119.23 | 4.95 | 1.0 | 0.03 | − | 0.000 | 0.000 |
| H3 | Habitat disturbance | 119.87 | 5.60 | 2.6 | 0.02 | 0.275 | 0.093 | 0.007 |

Model H5 (multivariate) included three variables: CONTIG_SD (Standard deviation of Contiguity Index), PROX_CV (Coefficient of variation of Proximity Index) and AREA_RA (Range of Patch Area; Appendix VI). CONTIG_SD (figure 14, A) and PROX_CV (figure 14, B) were positively related with the number of species that were specialists of open areas. Despite having a linear relationship, the former was less correlated with this group species richness than the latter (SpCor= 0.32 and 0.59, respectively). In turn, AREA_RA exhibited a nonlinear and negative relation with the species richness of this functional group (figure 14, C).

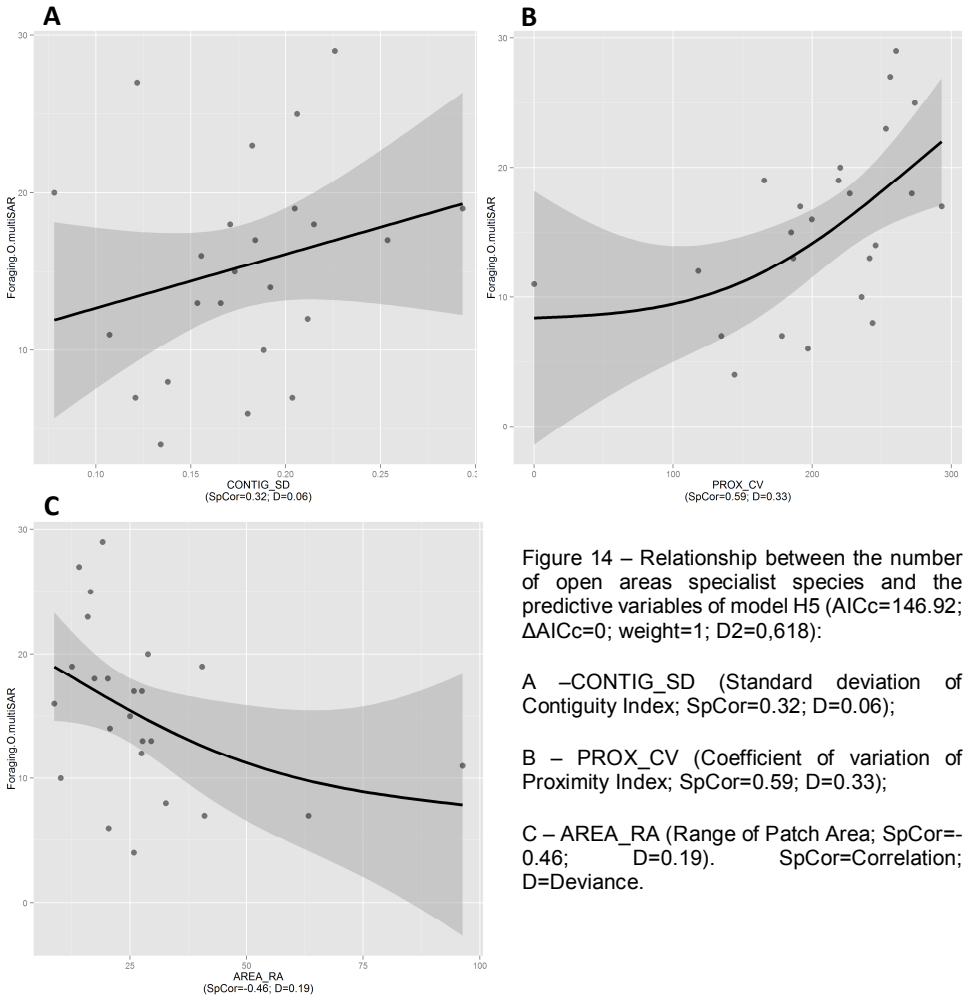


Figure 14 – Relationship between the number of open areas specialist species and the predictive variables of model H5 (AICc=146.92; ΔAICc=0; weight=1; D2=0,618):

A –CONTIG_SD (Standard deviation of Contiguity Index; SpCor=0.32; D=0.06);

B – PROX_CV (Coefficient of variation of Proximity Index; SpCor=0.59; D=0.33);

C – AREA_RA (Range of Patch Area; SpCor=-0.46; D=0.19). SpCor=Correlation; D=Deviance.

### *Number of Shrublands specialist species*

All the best performing models recorded a good performance to explain the distribution of shrubland specialist species richness (both observed and estimated), with corSp > 0.7 (table 10). Likewise, both presented high deviance ($D^2$) with $D^2$>0.5 (Table 10). Adjusted deviance ($adjD^2$) values were generally lower, with the model H5 based on SAR-estimated species richness presenting a lower value in comparison to H4 ($adjD^2_{H5}$=0.358 vs. $ajdD^2_{H4}$=0.362).

Hypotheses H4 and H5 were the most successful explaining the observed number of specialist species of this habitat with H4 having the higher Akaike weight (w=0.53) followed by H5 (w=0.36) (see table 10). Estimated values revealed, once again, a very high Akaike weight value of model H5 (w=0.72).

Table 10 – Results from Akaike's information criterion model ranking for number of bird species that inhabit shrublands. Competing models are ordered from best to least fit hypothesis by the AICc values. Models with ΔAIC < 2 are highlighted.

| Estimated values (SAR) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Hypothesis** | **AICc** | **ΔAICc** | **df** | **$w_i$** | **corSp** | **$D^2$** | **adj$D^2$** |
| H5 | Landscape structure | 113.43 | 0.00 | 4.5 | 0.72 | 0.736 | 0.525 | 0.358 |
| H1 | Climate & Topography | 116.22 | 2.78 | 3.7 | 0.18 | 0.671 | 0.455 | 0.340 |
| H4 | Landscape composition | 117.38 | 3.95 | 4.8 | 0.10 | 0.606 | 0.473 | 0.362 |
| H3 | Habitat disturbance | 132.57 | 19.13 | 2.9 | 0.00 | 0.351 | 0.165 | 0.085 |
| H2 | Habitat diversity | 138.97 | 25.54 | 2.5 | 0.00 | 0.250 | 0.049 | 0.000 |
| H0 | Null hypothesis | 139.04 | 25.61 | 1.0 | 0.00 | − | 0.000 | 0.000 |
| Observed values | | | | | | | | |
| | **Hypothesis** | **AICc** | **ΔAICc** | **df** | **$w_i$** | **corSp** | **$D^2$** | **adj$D^2$** |
| H4 | Landscape composition | 78.35 | 0.00 | 2.9 | 0.53 | 0.777 | 0.507 | 0.460 |
| H5 | Landscape structure | 79.10 | 0.76 | 4.4 | 0.36 | 0.709 | 0.574 | 0.424 |
| H1 | Climate & Topography | 82.30 | 3.96 | 3.0 | 0.07 | 0.601 | 0.395 | 0.268 |
| H3 | Habitat disturbance | 84.34 | 5.99 | 2.9 | 0.03 | 0.470 | 0.330 | 0.266 |
| H2 | Habitat diversity | 89.96 | 11.61 | 2.0 | 0.00 | 0.362 | 0.113 | 0.029 |
| H0 | Null hypothesis | 91.76 | 13.41 | 1.0 | 0.00 | − | 0.000 | 0.000 |

Model H5 was a multivariate model that consisted of the variables GYRATE_RA (Range of Radius of Gyration), CONTIG_SD (Standard deviation of Contiguity Index) and SPLIT (Splitting Index). The former variable showed a linear relationship with the number of shrublands specialist species (figure 15, A), contrary to CONTIG_SD, which exhibited a nonlinear relation with this group (figure 15, B).

However, both were positively related, even though weakly (SpCor= 0.25 and SpCor=0.32, respectively). In turn, the relationship between this specialist group richness and the variable SPLIT was linear and negative (figure 15, C).

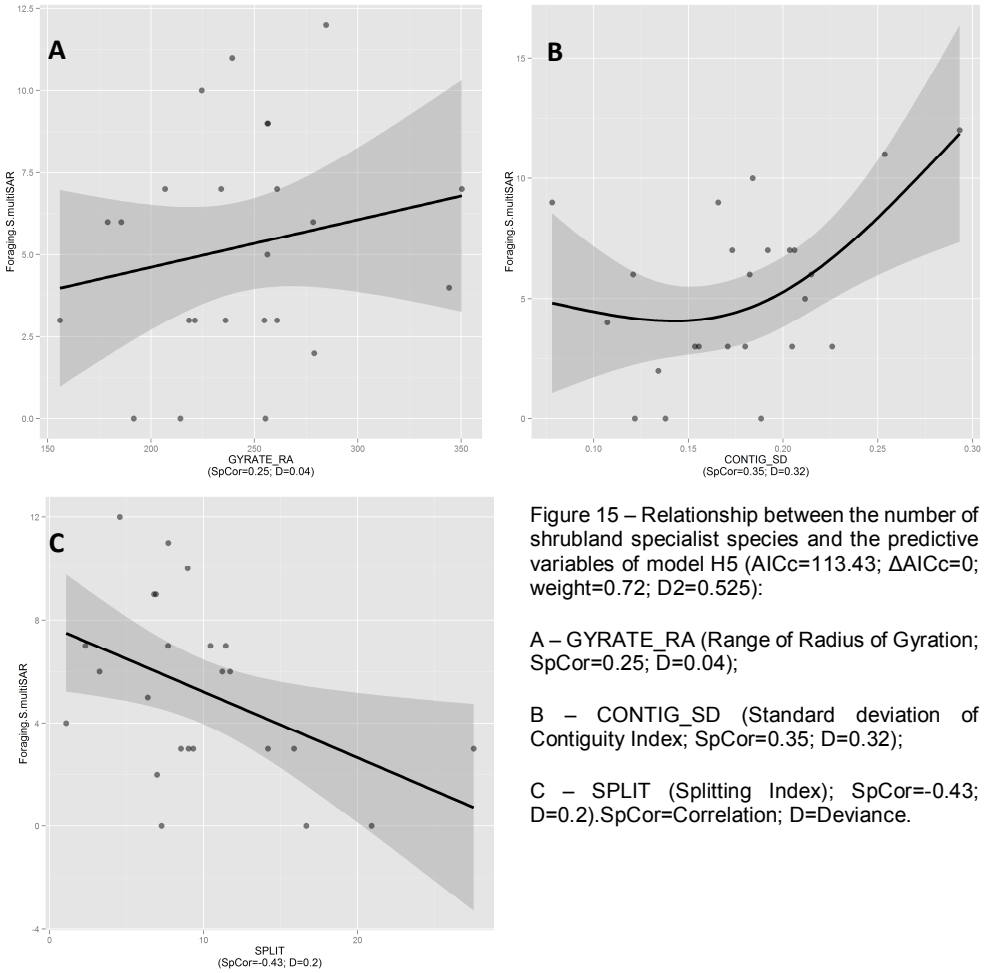


Figure 15 – Relationship between the number of shrubland specialist species and the predictive variables of model H5 (AICc=113.43; ΔAICc=0; weight=0.72; D2=0.525):

A – GYRATE_RA (Range of Radius of Gyration; SpCor=0.25; D=0.04);

B – CONTIG_SD (Standard deviation of Contiguity Index; SpCor=0.35; D=0.32);

C – SPLIT (Splitting Index); SpCor=-0.43; D=0.2).SpCor=Correlation; D=Deviance.

### *Number of Woodlands specialist species*

All the best performing models showed a reasonable performance to explain woodlands specialist species richness (both observed and estimated), with corSp > 0.6, with the exception of the model H1 of observed species richness (corSp=0.388). Regarding deviance (D2) and Adjusted deviance (adjD2), both models for SAR-estimated and observed species richness presented moderate to good values ($D^2$>0.5 and adj$D^2$>0.4), once again with the exception of model H1 of observed species richness ($D^2$=0.443 and adj$D^2$=0.390).

The most successful hypotheses explaining the number of woodland specialist species were H2 and H1 (table 11). Model H2 was distinctly the most explanative, with an Akaike weight equal to 0.51, comparatively to H1 (w=0.25).

When considering SAR-estimated values MMI produced similar results but with slightly higher Akaike weights (H2=0.58 and H1= 0.33) than those acquired with observed values.

Table 11 – Results from Akaike's information criterion model ranking for number of bird species that inhabit woodlands. Competing models are ordered from best to least fit hypothesis by the AICc values. Models with ΔAIC < 2 are highlighted.

| Observed values | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Hypothesis** | **AICc** | **ΔAICc** | **df** | **$w_i$** | **corSp** | **$D^2$** | **adj$D^2$** |
| H2 | Habitat diversity | 108.87 | 0.00 | 2.7 | 0.51 | 0.683 | 0.511 | 0.464 |
| H1 | Climate & Topography | 110.28 | 1.42 | 2.7 | 0.25 | 0.388 | 0.443 | 0.390 |
| H5 | Landscape structure | 111.16 | 2.29 | 2.0 | 0.16 | 0.720 | 0.344 | 0.282 |
| H4 | Landscape composition | 113.75 | 4.88 | 2.2 | 0.04 | 0.544 | 0.252 | 0.180 |
| H3 | Habitat disturbance | 115.59 | 6.73 | 2.7 | 0.02 | 0.690 | 0.213 | 0.138 |
| H0 | Null hypothesis | 116.99 | 8.12 | 1.0 | 0.01 | − | 0.000 | 0.000 |
| Estimated values (SAR) | | | | | | | | |
| | **Hypothesis** | **AICc** | **ΔAICc** | **df** | **$w_i$** | **corSp** | **$D^2$** | **adj$D^2$** |
| H2 | Habitat diversity | 132.11 | 0.00 | 3.5 | 0.58 | 0.780 | 0.532 | 0.433 |
| H1 | Climate & Topography | 133.23 | 1.12 | 3.9 | 0.33 | 0.628 | 0.527 | 0.427 |
| H5 | Landscape structure | 136.73 | 4.62 | 4.8 | 0.06 | 0.492 | 0.488 | 0.381 |
| H4 | Landscape composition | 138.53 | 6.42 | 3.1 | 0.02 | 0.605 | 0.359 | 0.224 |
| H3 | Habitat disturbance | 139.87 | 7.76 | 2.9 | 0.01 | 0.783 | 0.315 | 0.250 |
| H0 | Null hypothesis | 149.08 | 16.97 | 1.0 | 0.00 | − | 0.000 | 0.000 |

Model H2 (bivariate) was composed of variables hab_richness (Habitat richness) and sp_richplant (Plant species richness). The relationship between these variables and woodland specialist species richness was linear and positive (figure 16, A and B), with the former being highly correlated (SpCor=0.66). In turn, hab_richness was positively correlated with the percent cover of natural forest (SpCor=0.58; $p<0.05$). Model H1 consisted of variables Bio_15 (Coefficient of variation of Precipitation seasonality) and Bio_16 (Precipitation of wettest quarter). They both were nonlinearly related with this group species richness and presented a low correlation (figure 16, C and D).

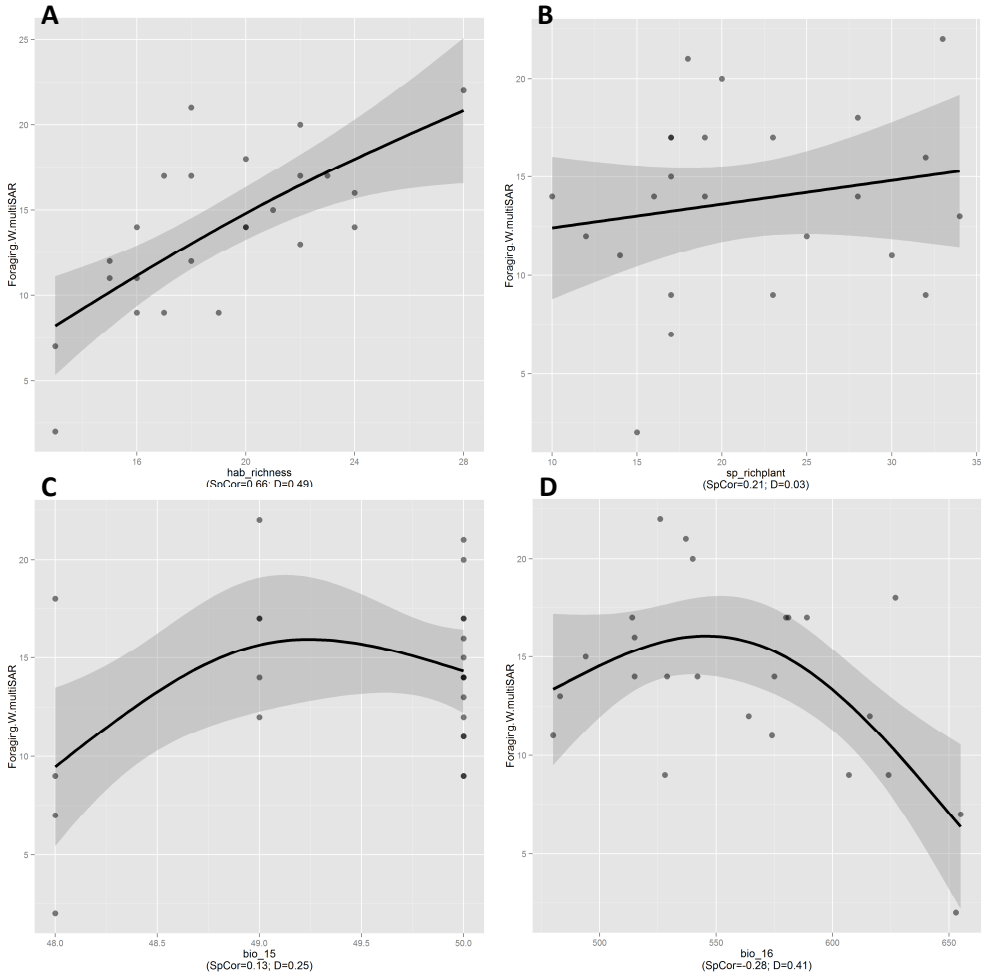


Figure 16 – Relationship between the number of woodland specialist species and the predictive variables of models H2 (AICc= 132.11; ΔAICc=0; weight=0.58; D2=0,532): A – hab_richness (Habitat richness; SpCor=0.66; D=0.49); B –sp_richplant (Plant species richness; SpCor=0.21; D=0.03); and model H1 (AICc= 133.23; ΔAICc=1.12; weight=0.33; D2=0,527): C – Bio_15 (Coefficient of variation of precipitation seasonality; SpCor=0.13; D=0.25); D – Bio_16 (Precipitation of wettest quarter; SpCor= -0.28; D=0.41). SpCor=Correlation; D=Deviance.

### 3.3. Overall comparison

Overall, Landscape structure (H5) was the most important landscape ecological factor determining passerine species richness considering its corresponding model was the most highly ranked and generated the highest Akaike weight values (Figure 17). In general, Akaike weight values of SAR- based models were less distributed across the response variables than those based on observed values, presenting high values for only few of them (Figure 17). However, the models with the highest Akaike weight values were often coincident between estimated and observed models.


Figure 17 – Barplots representing Akaike weight values (varying from 0.0 to 1.0) obtained by the models for each landscape ecological driver (H1 to H5) and considering observed (OBS) and SAR-estimated (SAR) passerine species richness for total, by feeding traits (insectivorous, granivorous and omnivorous), and, by foraging habitat traits (open area, shrublands and woodlands).

Further exploration, using Hierarchical Cluster Analysis, confirmed the importance of landscape structure (Figure 17, e), with total passerine species, granivorous and omnivorous species, as well as open area and shrubland habitat specialists being mostly sensible to this factor (Figure 18, group 1). In this group, omnivorous and open areas specialist species were the most similar groups, closely followed by total passerine species. More distant were shrublands specialist and granivorous species, with the latter being the group less similar to the others.

Habitat diversity also plays an important role, determining the number of insectivorous species and woodlands specialists (Figure 18, group 2).

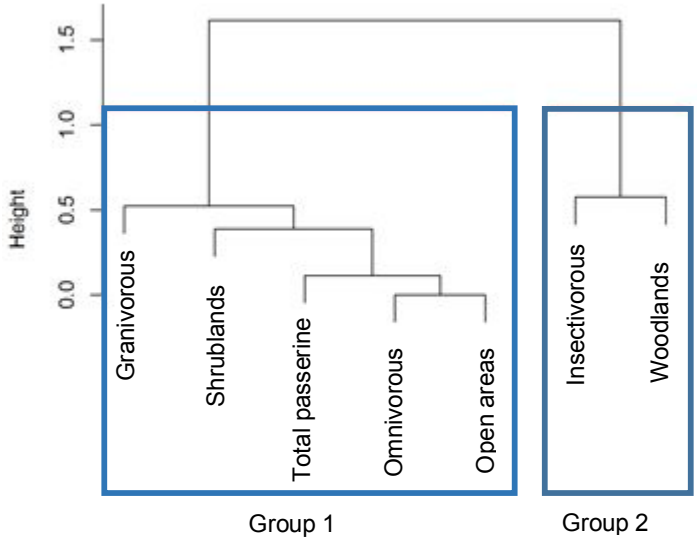


Figure 18 – Cluster dendrogram split in two groups. Hierarchical Cluster Analysis was applied with a Euclidean distance matrix calculated from Akaike weights summarizing the responses of each SAR-estimated variable to environmental drivers.

Passerine species richness divided by feeding habit revealed a few differences between groups regarding its most explanative ecological factors. While for granivorous and omnivorous groups landscape structure was the most determining factor of species richness (Figure 18, group 1 and 2), insectivorous species richness was better explained by landscape composition and habitat diversity variables (Figure 17, d; Figure 19, group 3). Also, granivorous species were the only group to present a strong relation with habitat disturbance (Figure 17, c; Figure 19, group 1).

Regarding foraging habitats, open area and shrubland specialist species once again exposed landscape structure's great importance for these species group (Figure 19, group 2). On the other hand, woodland specialist species stood out by being mainly

explained by not only habitat diversity variables but also by climate and topography, which did not happen for any other groups (Figure 17, a; Figure 19, group 4).

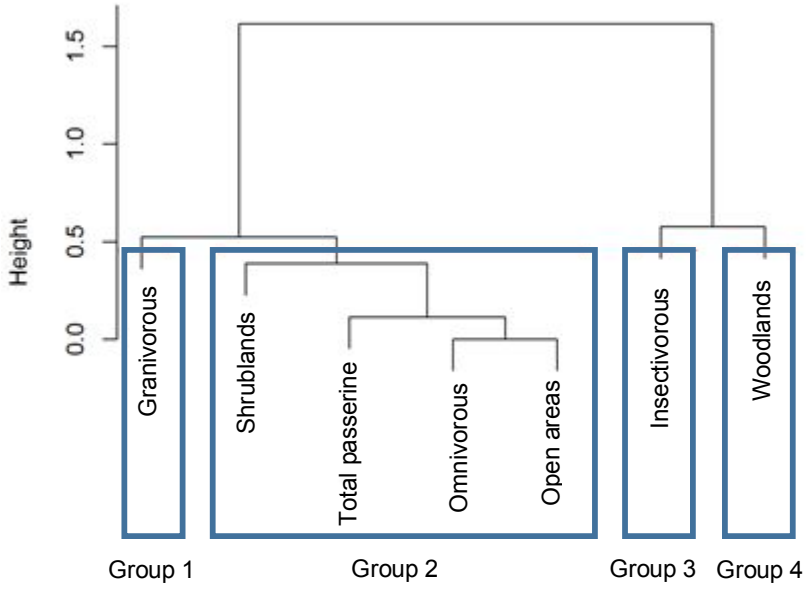


Figure 19 – Cluster dendrogram split in four groups. Hierarchical Cluster Analysis was applied with a Euclidean distance matrix calculated from Akaike weights summarizing the responses of each SAR-estimated variable to environmental drivers.

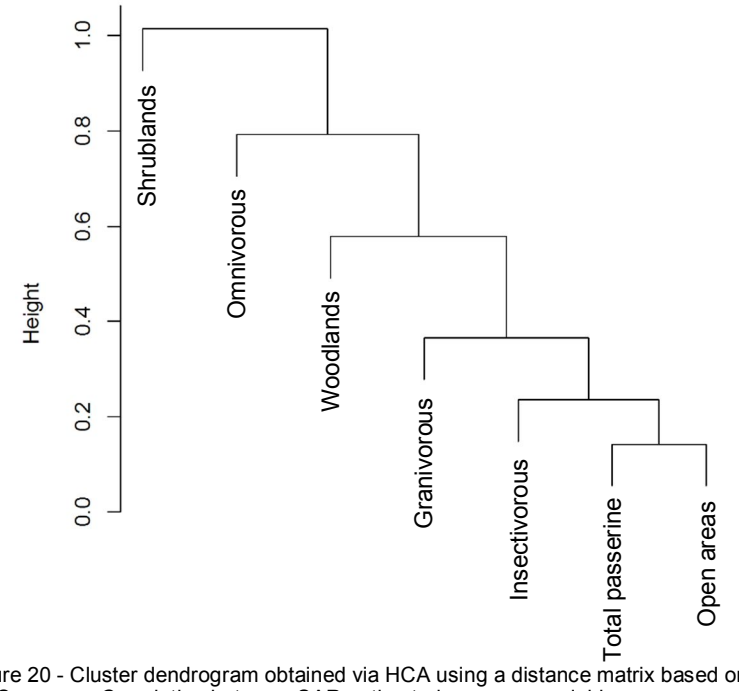


Figure 20 - Cluster dendrogram obtained via HCA using a distance matrix based on 1 – Spearman Correlation between SAR-estimated response variables.

The comparison between the structure of the cluster dendrograms calculated from the Akaike weights summarizing the responses of each variable to environmental drivers

(Figure 18 and 19) and the cluster dendrogram based on co-occurrence patterns of total species and/or species richness by feeding or habitat traits calculated using Spearman correlation values between the response variables (Figure 20) revealed a great distinction between them. As an example, even though total passerine and insectivorous species were grouped in close clusters in the latter dendrogram, they were on opposite positions of the first branches to differentiate in the former. This is an indication that the correlation between response variables did not majorly influence their responses to environmental drivers.

# 4. Discussion

## 4.1. Improving predictions of passerine species richness

Overall, results show that the developed models, supported by robust Multi-model Inference concepts, are good predictive tools allowing a clear perception of the influence of landscape ecological factors on passerine species richness. The correspondence between observed and SAR-estimated passerine species richness and the environmental variables, and the generally good model performance across response variables, suggests that the regression models adequately described species richness patterns.

The use of estimated values derived from Species-Area relationship provided an important contribution to minimize the effect of differences in sampling effort and therefore improving model performance (figure 9). In general, by using observed values, a higher number of models (between 1 and 5) were present in the confidence set ($\Delta AICc<2$) and with generally lower and similar weight values ($0.12 \leq w \leq 0.67$) comparatively to models using SAR-estimated values, which had only 1 or 2 models in the confidence set and, as expected, presented higher weight values ($0.33 \leq w \leq 1$). However, both were very congruent in the sense that the latter models were always present in the confidence set of the former, even though the ranking order often differed between the two. The results suggest that, by improving model predictive performance, the use of SAR estimated data is effective and a promising solution to bridge the gap of differential sampling efforts when studying species richness patterns as previously observed in similar studies (*e.g.* Borges et al., 2009; Hortal et al., 2004).

The use of combinations of predictive variables (based on a priori definition of competing hypothesis supported by previous research), for selecting the variables for each model also lead to the improvement of the models' predictive capacity and provided a general and flexible approach. A similar combinatorial approach, tested in Schindler

et al. (2015) has been found to perform better than other selection methods based on theoretical considerations, expert knowledge, previously published studies and statistical approaches aiming at the elimination of redundant variables and allowing the identification of potentially unnoticed associations between response and predictor variables when using the aforementioned methods. In addition, this method allowed the use of different variables belonging to the same group (with similar ecological meaning) and to select the best subset among these, focusing not on specific variables but on their ecological meaning and predictive performance. This methodology, focused on groups of explanatory variables with similar ecological meaning, may enable the comparison between analogous studies since the lack of consistency in using environmental variables oftentimes obstructs a ready comparison of methodologies and results (Qian, 2010).

### 4.2. Drivers of passerine species richness

Results showed that passerine species richness in the study area was mostly determined by landscape structure. It indicate that landscape attributes had an impact on biodiversity, similarly to the results obtained by Fahrig et al. (2011), Tscharntke et al. (2012) and Newbold et al. (2014).

In particular, the spatial aggregation of patches forming the landscape revealed to be determinant for the distribution of total passerine species richness. In particular, the size and proximity of those patches (Figure 10, B and A; Proximity Index and Effective Mesh Size, see Appendix VI) and its spatial connectedness (Figure 10, C; Contiguity index, see Appendix VI). Surprisingly, even though fragmentation has been frequently considered to have negative effects on biodiversity (Fahrig, 2003) the variables forming the best explanative model show a positive effect of fragmentation by benefiting from the presence of different patches instead of a dominating one (Figure 10, A and B). This may be explained by the fact that passerines include a diverse group of species with different foraging habitats, feeding habits, reproducing strategies, among others. Also, some passerine species require different habitats during different life stages either directly, for reproducing, or indirectly, to feed (*e.g.* accompanying the life cycle of insects). This heterogeneity implies a large spectrum of ecological requirements that a homogeneous landscape, with more limited resources, would potentially fail to provide.

The interdigitation of different habitat types is, in this case, positive because it increases landscape complementation by providing a wider range of food and shelter resources and reproducing sites (Fahrig et al., 2011), which allow the coexistence of a higher number of competing and non-competing species in the landscape (Atkinson and

Shorrocks, 1981; Fahrig, 2003; Wilson et al., 2004) and at the same time meet the patch size requirements of each individual species (Vance et al., 2003). This effect may also favor metapopulation dynamics, by reducing competition for the same resources, and species resistance (Hanski, 1999), by providing a wide range of substitute resources in case some seize to exist.

The heterogeneous distribution of patches as well as the diversity of their sizes were also associated with an increase in total species richness (Figure 10, B and C), most likely because it promotes the partitioning of limited resources. This partitioning leads to the increase of the number of places to nest, hide, feed, among others, thus preventing domination of a single competitor species (Huston and Huston, 1994).

Although with relatively less predictive performance, model ranking based on observed species richness ranked habitat diversity (H2) as the model with highest support (Table 5), which is in accordance with the previously discussed arguments, since habitat diversity entails diversity of resources and foraging habitats.

Similarly to the total passerine species richness, omnivorous and open areas specialist species richness were also strongly determined by landscape structure. In the case of omnivorous species, their species richness distribution was more specifically determined by the size of core area and area of the patches (Figure 13, A and B; Total Core Area and Perimeter-Area Ratio, appendix VI). According to the results, species richness of this group increase with the decrease of those variables, and is favored by the heterogeneity of the matrix. This goes in line with the previously discussed regarding total species richness and the ecological requirements of omnivorous species, since their diet is wide ranged and often changing seasonally, which allows them to take advantage of more food sources, granting better survival rates. In its turn, open area species richness decreased with increasing patch area range (Figure 14, C; Patch area, appendix VI) and increased with higher variation of the size and proximity of the patches (Figure 14, B; Proximity Index, appendix VI), which can be associated with urban-rural mosaic habitats. It also increased with spatial connectedness (Figure 14, A; Connectivity Index, appendix VI), more associated with contiguous mountain habitats, with bare rock and sparsely vegetated areas. This may be explained by the complexity and heterogeneity of species contained in this functional group, which includes passerines commonly linked to lowland urban-rural habitats (*e.g. Passer domesticus*, *Hirundo rustica* and *Serinus serinus)*, and different types of mountain mosaics (*e.g. Saxicola sp*., *Emberiza cia* and *Alauda arvensis)*.

Contrary to the groups above, shrubland specialist species, although determined by landscape structure, did not have a positive relationship with fragmentation (Figure 15,

C). For this group, species richness decreased with the increase of patch division (Split Index, appendix VI). Although previously recognized as edge species (Boulinier et al., 2001), evidence suggests they avoid edges (Schlossberg and King, 2008), which are a by-product of habitat fragmentation. These specialist species have a preference for large and continuous habitat patches of core shrubland/scrubland areas and thus, the presence of irregular patch shapes and edges can become a disturbance to them (Schlossberg and King, 2008; Shake et al., 2012).

Granivorous species was the only group significantly affected by habitat disturbance. The species richness of this group was positively related to areas that recorded changes in land cover/use in the last 20 years (Figure 12, B) but was negatively associated to wildfires that struck the landscape during those same years (Figure 12, A). As species that mainly feed on seeds and grain, they are dependent of the productivity and composition of grass and shrubs, since higher productivity leads to an increase of seed resource yielding (Franklin et al., 2005), which are affected by fire regimes (Crowley and Garnett, 1999; Lonsdale et al., 1998; Russell-Smith et al., 2003). The continuous incidence and long exposure to fire disturbance can become detrimental to the survival and growth of grasses and their seed (*e.g.* Crowley and Garnett, 1999). This is especially relevant for the Vez watershed due to the extent and frequency of wildfires, which occurred almost every year in this area, eight of which registered more than 10 $km^2$ of total burnt area (National Cartography of Burnt Areas 1990-2012, ICNF). In accordance, the land cover change that has been occurring in the last two decades has been induced by fire (mostly in shrublands and forest areas) and land abandonment (mainly of marginal/less productive crop areas in the higher regions), which may have given rise to new shrubland areas. This reveals that this species group may have a strong sensibility to that habitat, being highly correlated and favored by its availability (figure 12, B). The positive link between granivorous passerines and more dynamic landscapes also suggests that these species may be benefited by semi-natural vegetation types following farmland abandonment over the last two decades.

Woodland specialists and insectivorous species were the only groups being predominantly determined by habitat diversity and not landscape structure. They were both strongly and positively affiliated with the number of land cover types, different habitats and plant species present in the landscape (figure 11A and figures 16, A and B, respectively). Rather than its spatial distribution or aggregation, it was the presence of a great variability and diversity of habitats that promoted a higher number of different species of these groups.

Habitat diversity was also positively correlated to landscape mosaics with larger proportion of natural forests potentially benefiting woodland species.

However, insectivorous species also revealed an association to some habitat types. They showed a preference for natural forests even when in relatively low percentage cover and showed a decrease in species richness when production forest increases (figure 11, B and C). Most likely this is due to the abundant number of arthropod species present in native forests (Paoletti et al., 1989; Pimentel and Warneke, 1989), which decreases in production forest since these ecosystems are highly disturbed, often stripped of important habitats like deadwood, and are composed of younger trees.

In summary, even though all the accounted factors have influence on the distribution of passerine species richness, results show that, when accounting for their independent effects, each factor has different degrees of importance depending on the species group under examination.

Overall, landscape structure and habitat diversity were the most important landscape ecological factors determining the spatial variation in passerine species richness, similarly to the results of Schouten et al. (2009) and Schindler et al. (2013). Surprisingly, the independent effect of landscape structure (in particular fragmentation) evidenced in this study was more determinant to explain species richness than landscape composition, contrary to what was found in previous research evaluating the independent effects of landscape structure and landscape composition (Carrara et al., 2015; Fahrig, 2003; Smith et al., 2011). This could be because, even though the denomination 'landscape structure' is the same, the variables used in each study reflect different aspects. Despite being classified as landscape structure metrics, some metrics selected for our models revealed the inter-relation between habitat diversity and spatial attributes related to landscape configuration and composition. As such, these metrics provide a description and a numeric synthesis regarding several facets of the landscape structure. When used in analysis, the metrics are frequently selected *a priori,* not taking into account model performance. By selecting variables using combinations (step 1 of modelling framework), our methodology improved this aspect and may have positively influenced the relative relevance of these variables in the models.

Also taking into account the importance of heterogeneity and diversity of the landscape, this difference could be due to the different degree of specialization of the species comprising the functional groups and the generalist nature of their majority (total species, omnivorous species, open areas and shrublands specialist species).

Fragmentation and heterogeneity can be detrimental to species richness, reducing spatial and functional connectivity of natural habitat patches and leading to its conversion

and deterioration (Tews et al., 2004), and thus limiting or impeding biotic interactions intra/inter-species and reducing access to different resources. However, Vez watershed is mostly a rural area, with many woodland areas and crops, so it seems that functional connectivity remains relatively well. In addition, birds are highly mobile, so they are not as sensible as other taxa.

Climate and topography revealed to be the hypothesis with less relative support for explaining passerine species richness. The same was found by Schouten et al. (2009) and Maes et al. (2005), where variables related to heterogeneity of the environment were more strongly correlated with species richness. This could be due to the scale of these variables, with the aforementioned being regional, unlike the variables of the following hypothesis, which are local (Vicente et al., 2014) and thus translate more detailed aspects of the landscape correlated to passerine species richness gradients. This result shows that, although climate change affects species richness, local land use changes have a more direct and stronger impact on it at a local scale, as previously described by Willis and Whittaker (2002). Although climate is not the main driver of species richness at the local scale of this study, its impact is broader and indirectly present in habitat diversity and composition by influencing vegetation growth, reproduction and overall productivity (Hawkins et al., 2003).

In this study, the different factors were separated in order to simplify analysis and prioritize further future conservation studies or actions. However, as Commoner (1971) wrote "*Everything is connected to everything else",* so hypotheses can be difficult to disentangle, particularly since they are not mutually exclusive. As previously found before, spatial distribution of species richness is most likely the result of a combination of several factors and/or mechanisms, no single one can adequately explain all variation (Gaston and Lawton, 1990; Schouten et al., 2009). Although our focus was to assess and rank the independent contribution of each factor group, we suggest that improved predictions may be attained by combining models with greater support through multi-model averaging procedures (Burnham and Anderson, 2002; Symonds and Moussalli, 2011).

### 4.3. Contributions to management and conservation: aggregate sets of indicators based on passerine species responses to environmental drivers

By originating models with a good performance and revealing distinct environmental preferences, passerine species confirmed their value as ecological indicator species. The different passerine groups, based on feeding habits and foraging habitats, were

sensitive to distinctive landscape environmental factors, which shows they can be used to monitor and detect changes in the landscape. Based on these results we suggest three different indicators: (i) open area specialist species richness, (ii) granivorous species richness, and, (iii) insectivorous species richness.

This suggestion took into account, primarily, the hierarchical clustering analysis based on the response of these groups to environmental drivers (see Figure 19). Due to the frequent occurrence of wildfires in the Vez watershed, monitoring granivorous species richness would be a useful tool to manage and assess the ecological impact of this threat in the landscape, given this group's sensitivity to disturbance induced by wildfires or land use/cover changes. In turn, insectivorous species and open areas specialist species can provide information regarding landscape's habitat diversity and structure, respectively.

Simultaneously, we also based this selection on the cluster dendrogram based on co-occurrence patterns of species richness (see Figure 20), choosing the closest groups. This combined information allowed the selection of the three different groups that not only are indicators of different landscape ecological factors, but also that tend to co-occur in similar areas. This co-occurrence is, in this case, highly advantageous, because it allows the survey of the multiple indicators in the same sampling points. Even though total passerine species richness do not necessarily require previous knowledge of passerines feeding habits and foraging habitat, these functional groups lead to a more parsimonious survey, requiring the recording of less species.

In order to preserve and maintain high species richness values, first and foremost, is necessary to stop or greatly reduce habitat loss and increase habitat quality. Different species use distinct habitat types and need different amounts of habitat in order to persist (Fahrig, 2001; Fahrig, 2003). In turn, based on our results, it would be beneficial the adoption of management practices promoting heterogeneous and diverse patches, instead of extensive homogeneous ones (Gil-Tena et al., 2007; Schindler et al., 2013). Several examples in landscapes of different parts of the Mediterranean biodiversity hotspot (Myers et al., 2000) also found the preservation of a mosaic landscape type to be crucial for biodiversity conservation (Atauri and de Lucio, 2001; Rocchini et al., 2006; Torras et al., 2008). This diversity not only provides a multitude of resources and shelter, meeting the ecological needs of a large number of functional groups, and thus, favoring functional redundancy (Tscharntke et al., 2012), but it also can be an insurance against environmental changes (Parsche et al., 2011). However, the introduction of environmental heterogeneity should be evaluated carefully, taking into account that environment is experienced differently between different species and the conditions that

benefit one species may be harmful or have no effect for others (Schouten et al., 2009; Tews et al., 2004). The ability to provide functional insurance depends, among others, on the species ability to cross habitat boundaries present in fragmented landscapes (Tscharntke et al., 2012). Also, maintaining multiple species in ecosystems may improve its resilience and resistance to external shocks, as well as its capacity to provide ecosystem services since the presence of different species can fulfil similar ecological roles (Tscharntke et al., 2005) and this functional redundancy increases the chances of a given ecological role still be executed if a species becomes rare or extinct (Elmqvist et al., 2003; Folke et al., 2004).

## 5. Conclusion

This study not only provided valuable information on the drivers of species richness, but also originated a flexible methodology, capable of identifying species groups (in our case, passerine species partitioned by feeding or habitat traits) related to the ecological state of the landscape.

Being impossible to conserve the total area of ecosystems, many times strategies aim to define conservation priority areas according to its species richness, which highlights the necessity to improve the understanding of ecosystems functioning of the areas to be preserved, in order to improve land management.

The models created in this study, albeit simple and generic, and its posterior analysis, provide a useful insight regarding the relationship between passerine species richness and their surrounding environment – what drivers affect them and how much – and may help prioritize conservation areas or management actions.

Thus, an important step towards developing robust conservation measures, that take into account the impact of current environmental disturbances on species richness, is to investigate and rank the influence of landscape variables in species diversity. Once we are able to identify patterns in species richness and the decisive environmental factors underlying these patterns, it is then possible to use this information to develop the necessary actions and policies to effective and efficiently protect biodiversity.

Integrating passerine species richness monitoring into landscape management plans using the suggested indicators would be prolific, since they could enable the parsimonious measure of the effects of landscape change and disturbance, at a low cost and in a short time, and allow the evaluation of the effects of management and conservation policies with impacts on land use and landscape patterns and processes (Schindler et al., 2013).

By being a simple, understandable and effective methodology, the modelling framework developed in this study can be easily and quickly integrated with land management policies, not requiring highly specialized technicians and being apprehended by local stakeholders without major difficulty. Money and time are thus spared, which meets the political and economic demands currently made when facing environmental decisions.

Finally, we argue that the methodology developed in this study, combining modelling results from multi-model inference techniques and hierarchical cluster analysis, may be extended to other taxonomic groups, regions and environmental factors. This can not only lead to possible future investigations but can also help to define priority conservation actions and guide management and policy makers to make the best ecological decisions when facing budget and time constraints.

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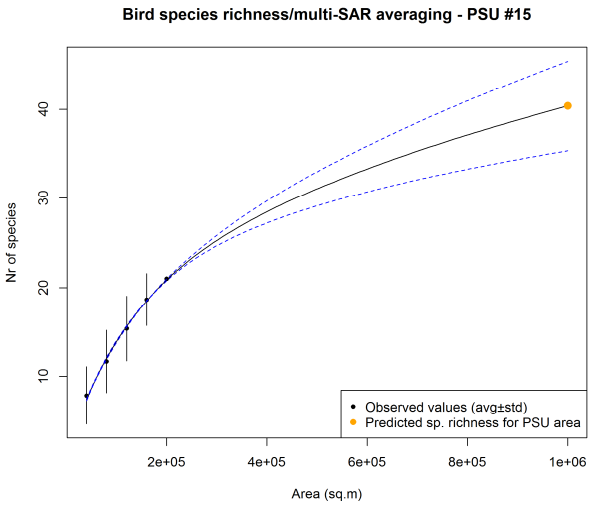
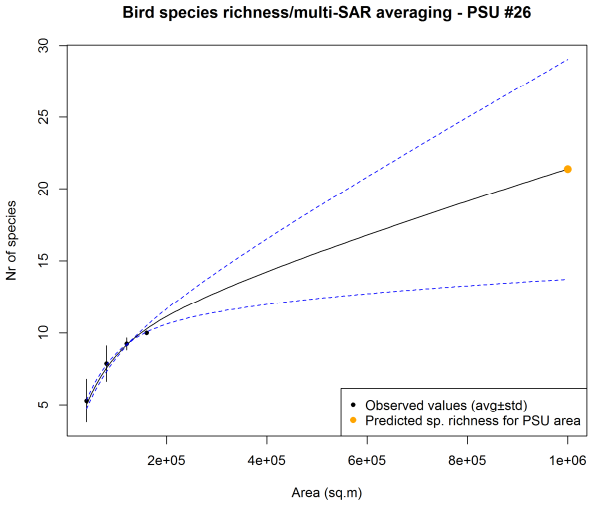
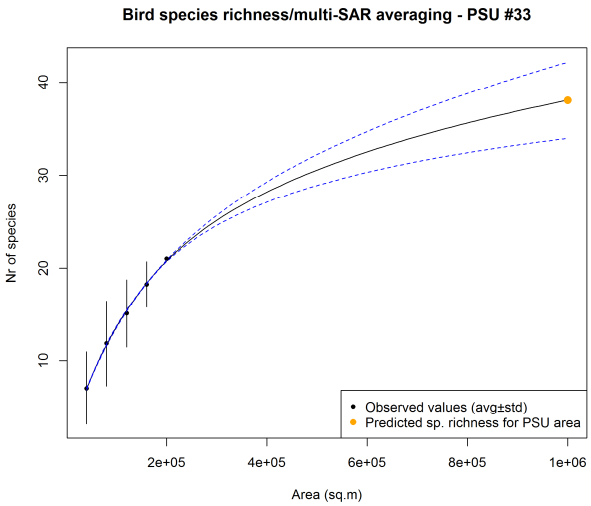
# Appendices

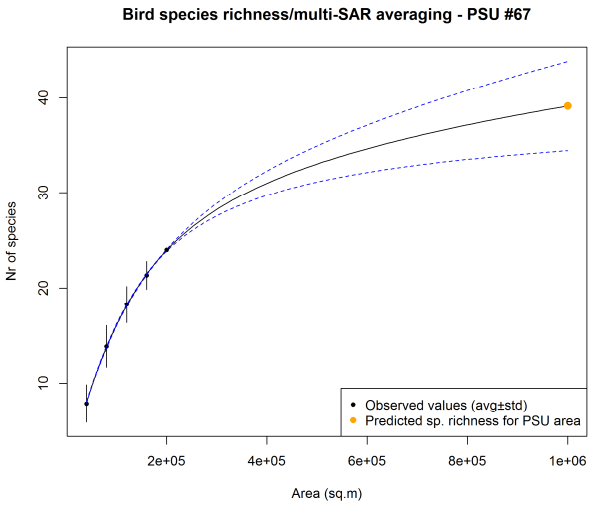
## Appendix I. Species-area relationship curve graphics

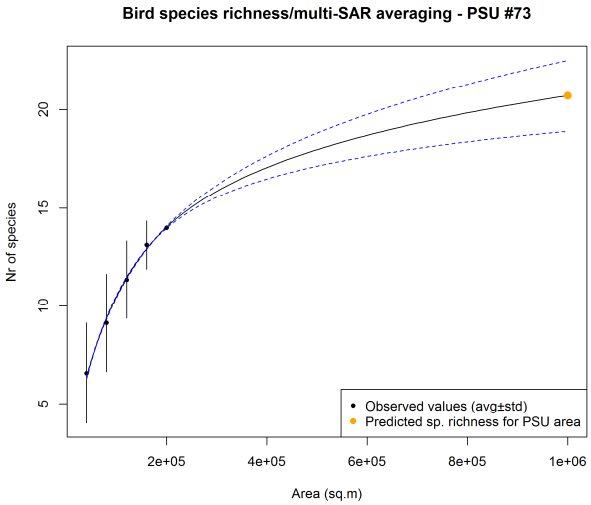
Species-Area relationship curve graphics used to estimate passerine species richness in the Primary Sampling Units.

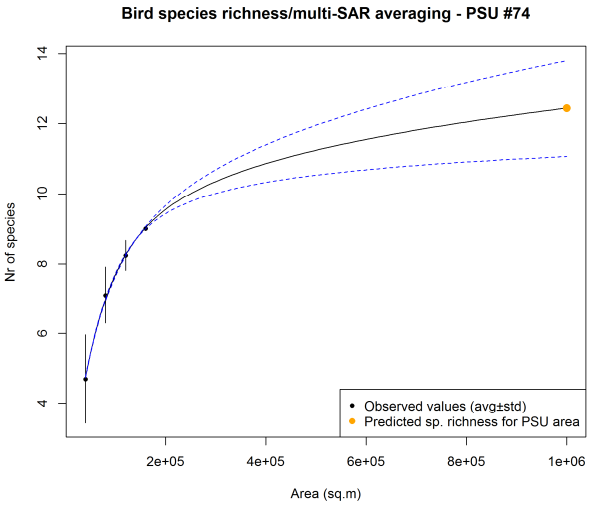


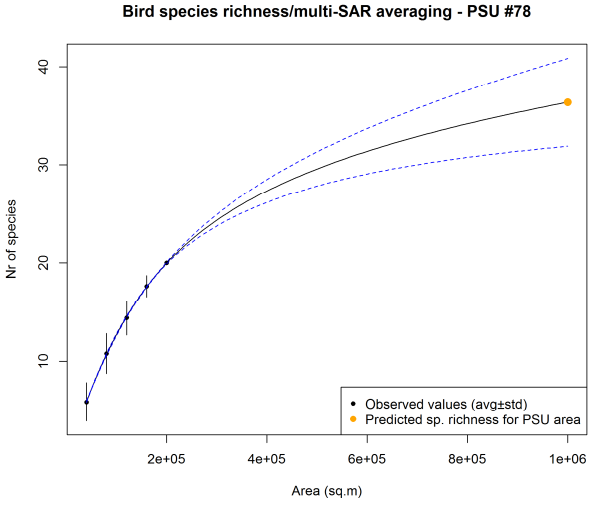



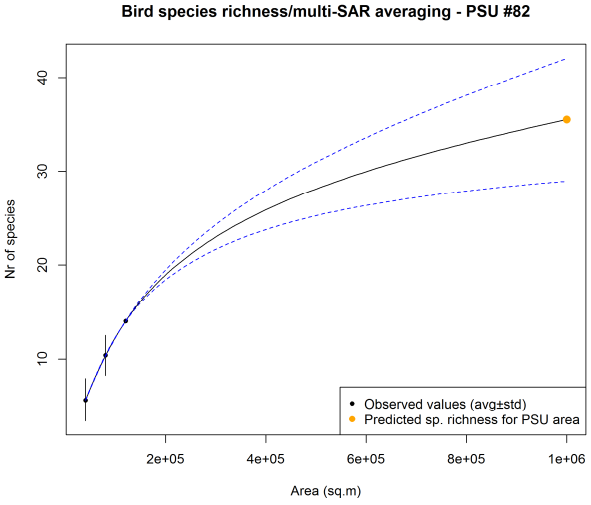



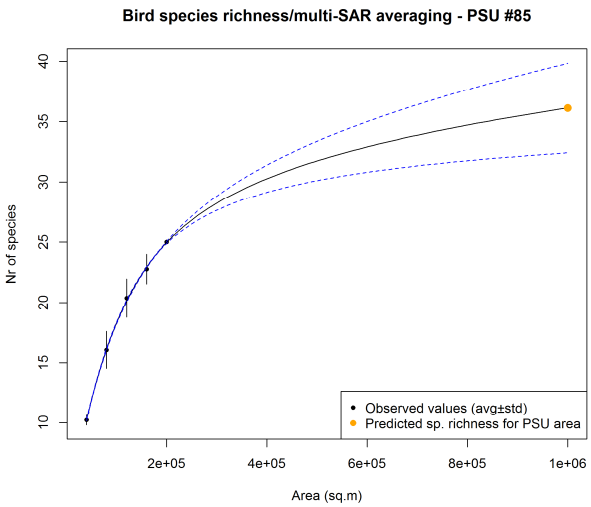



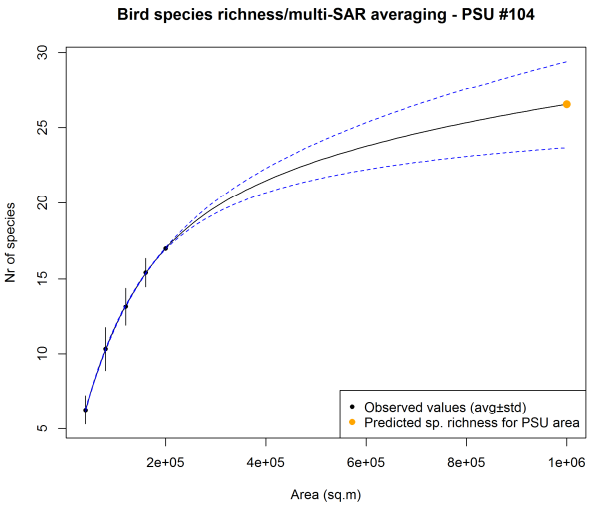

Bird species richness/multi-SAR averaging - PSU #73
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area

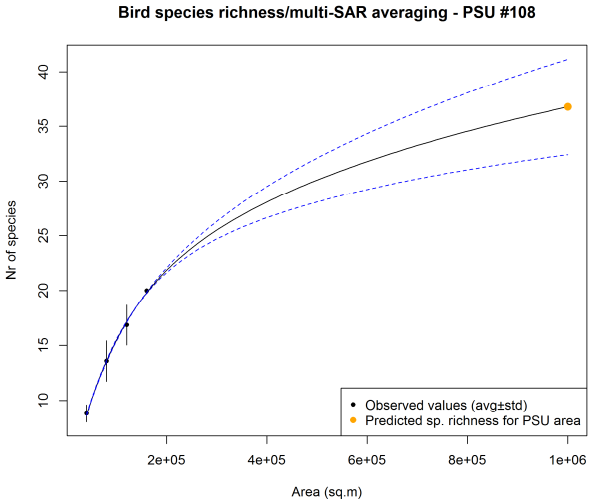

Bird species richness/multi-SAR averaging - PSU #74
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area

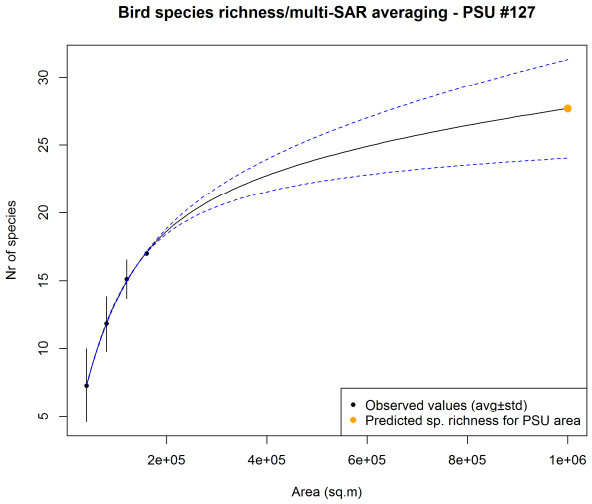

Bird species richness/multi-SAR averaging - PSU #78
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area

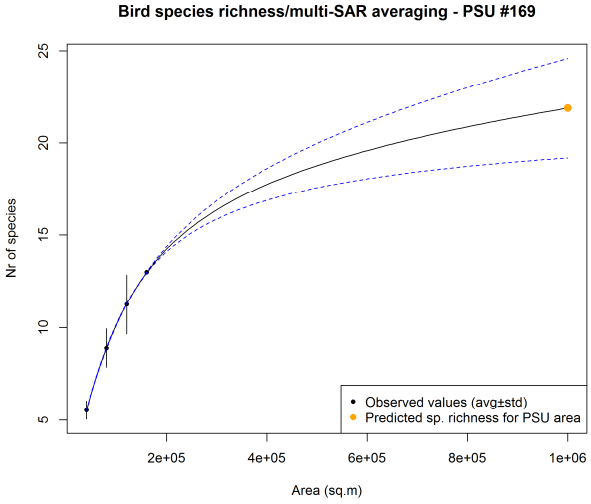

Bird species richness/multi-SAR averaging - PSU #82
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area

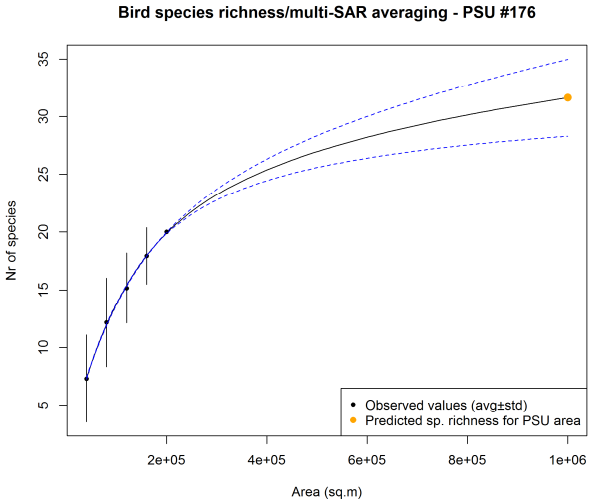

Bird species richness/multi-SAR averaging - PSU #85
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area

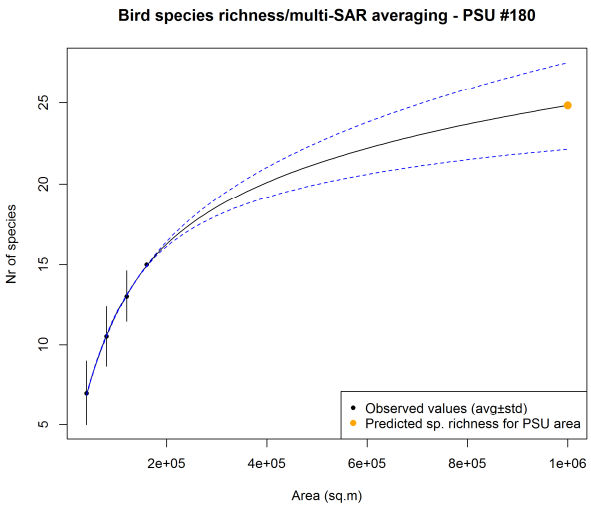

Bird species richness/multi-SAR averaging - PSU #104
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area

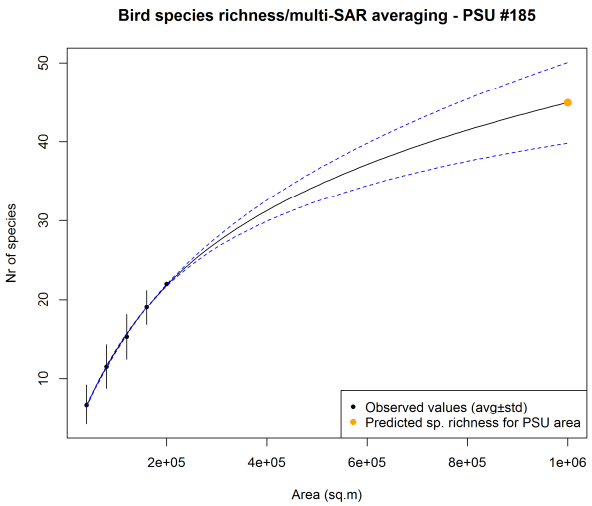

Bird species richness/multi-SAR averaging - PSU #108
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area

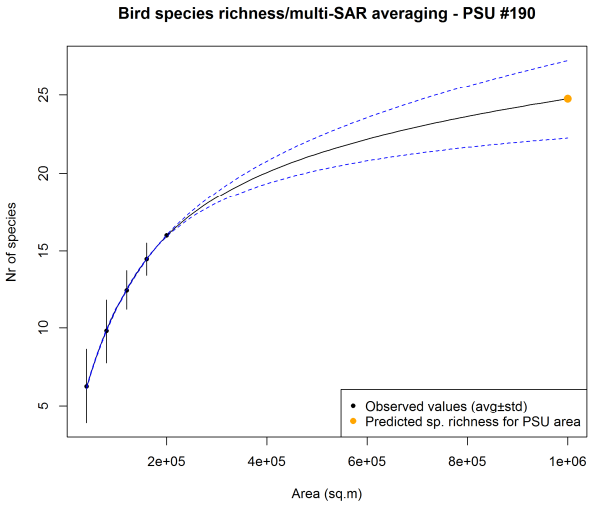

Bird species richness/multi-SAR averaging - PSU #127
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area

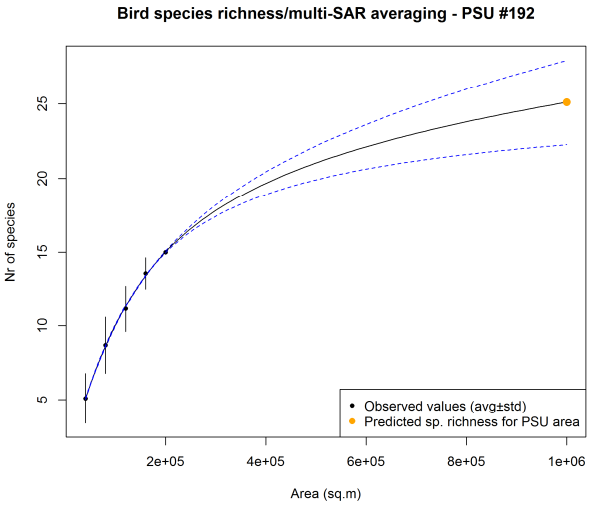

Bird species richness/multi-SAR averaging - PSU #169
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area

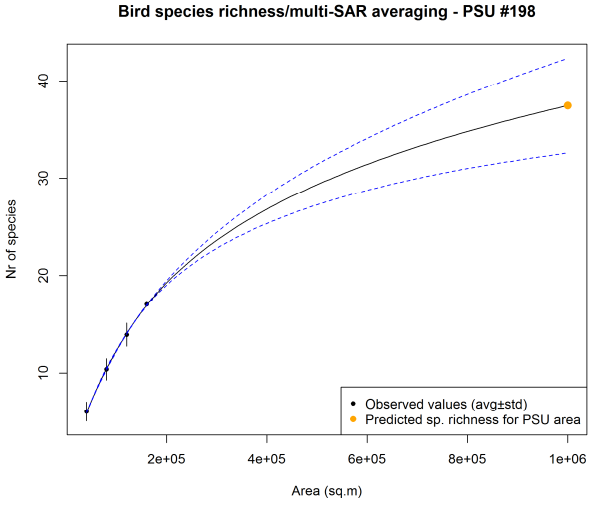

Bird species richness/multi-SAR averaging - PSU #176
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area

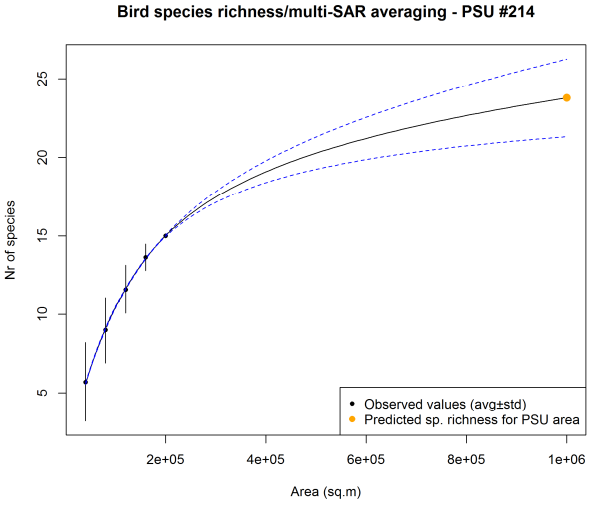

Bird species richness/multi-SAR averaging - PSU #180
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area

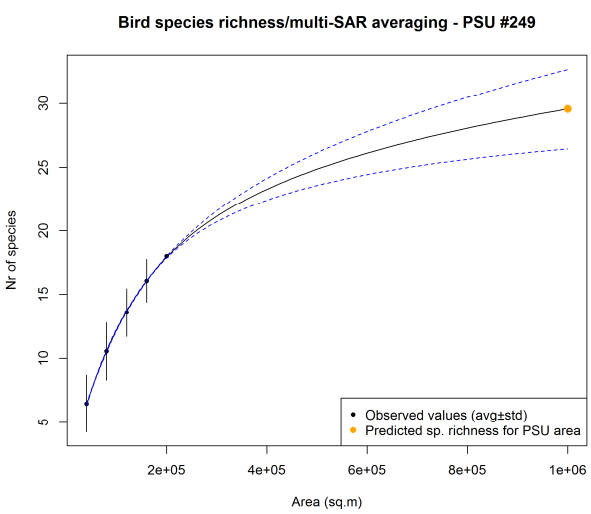

Bird species richness/multi-SAR averaging - PSU #185
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area

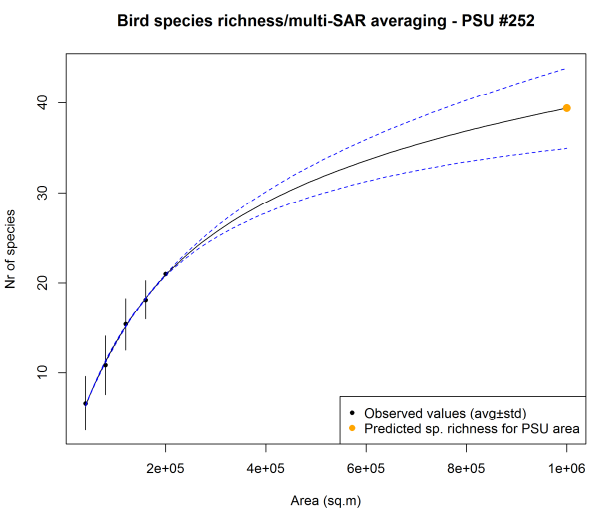

Bird species richness/multi-SAR averaging - PSU #190
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area

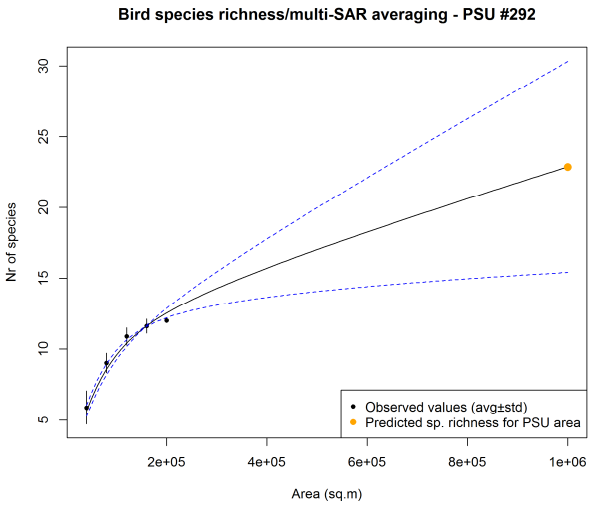

Bird species richness/multi-SAR averaging - PSU #192
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area

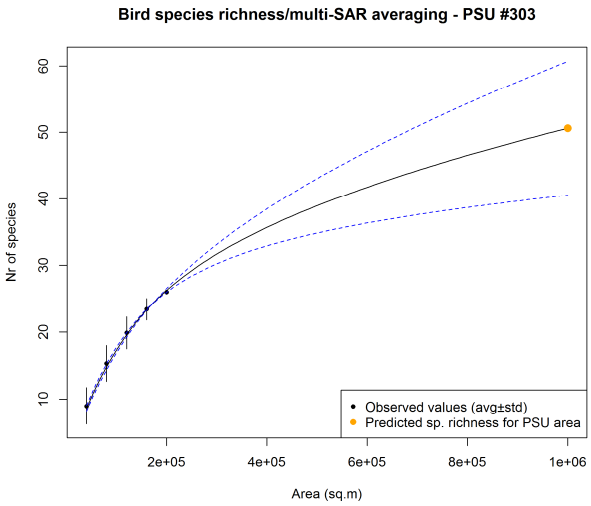

Bird species richness/multi-SAR averaging - PSU #198
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area


Bird species richness/multi-SAR averaging - PSU #214
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area


Bird species richness/multi-SAR averaging - PSU #249
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area


Bird species richness/multi-SAR averaging - PSU #252
Nr of species
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area


Bird species richness/multi-SAR averaging - PSU #292
Nr of species
5
10
15
20
25
30
2e+05
4e+05
6e+05
8e+05
1e+06
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area


Bird species richness/multi-SAR averaging - PSU #303
Nr of species
10
20
30
40
50
60
2e+05
4e+05
6e+05
8e+05
1e+06
Area (sq.m)
Observed values (avg±std)
Predicted sp. richness for PSU area

## Appendix II. Models selected in the modelling framework

| Response variable | Hypothesis | Predictors code | Predictors description |
|---|---|---|---|
| **Observed passerine species richness** | H1 - Climate & Topography | BIO_16 | Precipitation of wettest quarter (mm) |
| | | Elev_SD | Elevation (standard deviation) (m) |
| | H2 - Habitat diversity | hab_richness | Habitat richness |
| | H3 - Habitat disturbance | COS90_12_Cat_Change | Cover of areas that changed the land cover/use category between 1990-2012 |
| | H4 - Landscape composition | built_up_areas | Cover of built up areas (m) |
| | | natural_forest | Cover of natural forest (m) |
| | H5 - Landscape structure | PROX_CV | Proximity Index (Coefficient of variation) |
| **Observed number of insectivorous species** | H1 - Climate & Topography | Slope_MN | Slope (mean value for the 1km2 square (%) |
| | H2 - Habitat diversity | hab_richness | Habitat richness |
| | H3 - Habitat disturbance | COS90_12_Cat_Change | Cover of areas that changed the land cover/use category between 1990-2012 |
| | H4 - Landscape composition | natural_forest | Cover of natural forest (m) |
| | H5 - Landscape structure | PROX_CV | Proximity Index (Coefficient of variation) |
| **Observed number of granivorous species** | H1 - Climate & Topography | BIO_16 | Precipitation of wettest quarter (mm) |
| | H2 - Habitat diversity | hab_richness | Habitat richness |
| | H3 - Habitat disturbance | COS90_12_Cat_Change | Cover of areas that changed the land cover/use category between 1990-2012 |
| | H4 - Landscape composition | built_up_areas | Cover of built up areas (m) |
| | H5 - Landscape structure | PROX_CV | Proximity Index (Coefficient of variation) |
| **Observed number of omnivorous species** | H1 - Climate & Topography | BIO_15 | Precipitation seasonality (coefficient of variation) (mm) |
| | | BIO_17 | Precipitation of driest quarter (mm) |
| | H2 - Habitat diversity | h_habitats | Shannon index of habitat types |
| | H3 - Habitat disturbance | BurntPercMN_03_12 | Average 2003 - 2012 burnt area percentage (%) |

| | | | |
|---|---|---|---|
| | H4 - Landscape composition | bare_rock | Cover of bare rock areas (m) |
| | | scrub_and_sparsely_vegetated | Cover of scrub and sparsely vegetated areas (m) |
| | H5 - Landscape structure | AREA_MN | Patch Area (Mean) |
| | | SPLIT | Splitting Index |
| **Observed number of open areas specialist species** | H1 - Climate & Topography | BIO_16 | Precipitation of wettest quarter (mm) |
| | H2 - Habitat diversity | h_habitats | Shannon index of habitat types |
| | H3 - Habitat disturbance | COS90_12_Cat_Change | Cover of areas that changed the land cover/use category between 1990-2012 |
| | H4 - Landscape composition | annual_crops | Cover of annual crops (m) |
| | | built_up_areas | Cover of built up areas (m) |
| | H5 - Landscape structure | AREA_AM | Patch Area (Mean) |
| **Observed number of shrublands specialist species** | H1 - Climate & Topography | Slope_MN | Slope (mean value for the 1km2 square (%) |
| | | Slope_SD | Slope (standard deviation) |
| | H2 - Habitat diversity | h_habitats | Shannon index of habitat types |
| | H3 - Habitat disturbance | BurntPercMN_90_12 | Average 1990 - 2012 burnt area percentage (%) |
| | H4 - Landscape composition | built_up_areas | Cover of built up areas (m) |
| | H5 - Landscape structure | GYRATE_RA | Radius of Gyration (Range) |
| | | CONTIG_SD | Contiguity Index (Standard deviation) |
| | | SPLIT | Splitting Index |
| **Observed number of woodlands specialist species** | H1 - Climate & Topography | BIO_02 | Mean diurnal range (Mean of monthly (max temp - min temp) (ºC) |
| | H2 - Habitat diversity | hab_richness | Habitat richness |
| | H3 - Habitat disturbance | COS90_12_Cat_Change | Cover of areas that changed the land cover/use category between 1990-2012 |
| | H4 - Landscape composition | natural_forest | Cover of natural forest (m) |
| | H5 - Landscape structure | ENN_MN | Euclidean Nearest Neighbor Distance (Mean) |

| Response variable | Hypothesis | Predictors code | Predictors description |
|---|---|---|---|
| **Estimated passerine species richness** | H1 - Climate & Topography | BIO_04 | Temperature seasonality (Standard deviation*100) (ºC) |
| | | BIO_17 | Precipitation of driest quarter (mm) |
| | | Elev_SD | Elevation (standard deviation) (m) |
| | H2 - Habitat diversity | hab_richness | Habitat richness |
| | H3 - Habitat disturbance | COS90_12_Cat_Change | Cover of areas that changed the land cover/use category between 1990-2012 |
| | H4 - Landscape composition | annual_crops | Cover of annual crops (m) |
| | | built_up_areas | Cover of built up areas (m) |
| | H5 - Landscape structure | CONTIG_SD | Contiguity Index (Standard deviation) |
| | | PROX_CV | Proximity Index (Coefficient of variation) |
| | | MESH | Effective Mesh Size |
| **Estimated number of insectivorous species** | H1 - Climate & Topography | BIO_04 | Temperature seasonality (Standard deviation*100) (ºC) |
| | | BIO_06 | Min temperature of coldest month (ºC) |
| | | Elev_SD | Elevation (standard deviation) (m) |
| | H2 - Habitat diversity | h_habitats | Shannon index of habitat types |
| | H3 - Habitat disturbance | COS90_12_Cat_Change | Cover of areas that changed the land cover/use category between 1990-2012 |
| | | BurntPercMN_03_12 | Average 2003 - 2012 burnt area percentage (%) |
| | H4 - Landscape composition | natural_forest | Cover of natural forest (m) |
| | | production_forest | Cover of production forest (m) |
| | H5 - Landscape structure | PROX_CV | Proximity Index (Coefficient of variation) |
| **Estimated number of granivorous species** | H1 - Climate & Topography | Elev_SD | Elevation (standard deviation) (m) |
| | | Slope_SD | Slope (standard deviation) |
| | H2 - Habitat diversity | hab_richness | Habitat richness |
| | H3 - Habitat disturbance | COS90_12_Cat_Change | Cover of areas that changed the land cover/use category between 1990-2012 |
| | | BurntPercMN_90_12 | Average 1990 - 2012 burnt area percentage (%) |
| | | production_forest | Cover of production forest (m) |

| | | | |
|---|---|---|---|
| | H4 - Landscape composition | scrub_and_sparsely_vegetated | Cover of scrub and sparsely vegetated areas (m) |
| | H5 - Landscape structure | GYRATE_RA | Radius of Gyration (Range) |
| | | CONTIG_SD | Contiguity Index (Standard deviation) |
| | | SPLIT | Splitting Index |
| **Estimated number of omnivorous species** | H1 - Climate & Topography | BIO_02 | Mean diurnal range (Mean of monthly (max temp - min temp)) (ºC) |
| | | BIO_04 | Temperature seasonality (Standard deviation*100) (ºC) |
| | | Slope_SD | Slope (standard deviation) |
| | H2 - Habitat diversity | h_habitats | Shannon index of habitat types |
| | H3 - Habitat disturbance | BurntPercMN_90_12 | Average 1990 - 2012 burnt area percentage (%) |
| | | BurntPercMN_08_12 | Average 2008 - 2012 burnt area percentage (%) |
| | H4 - Landscape composition | bare_rock | Cover of bare rock areas (m) |
| | | production_forest | Cover of production forest (m) |
| | | scrub_and_sparsely_vegetated | Cover of scrub and sparsely vegetated areas (m) |
| | H5 - Landscape structure | PARA_RA | Perimeter - Area Ratio (Range) |
| | | CONTIG_SD | Contiguity Index (Standard deviation) |
| | | CORE_AM | Core Area (Area weighted mean) |
| **Estimated number of open areas specialist species** | H1 - Climate & Topography | BIO_04 | Temperature seasonality (Standard deviation*100) (ºC) |
| | | BIO_06 | Min temperature of coldest month (ºC) |
| | H2 - Habitat diversity | h_habitats | Shannon index of habitat types |
| | H3 - Habitat disturbance | COS90_12_Cat_Change | Cover of areas that changed the land cover/use category between 1990-2012 |
| | H4 - Landscape composition | bare_rock | Cover of bare rock areas (m) |
| | | production_forest | Cover of production forest (m) |
| | H5 - Landscape structure | AREA_RA | Patch Area (Range) |
| | | CONTIG_SD | Contiguity Index (Standard deviation) |
| | | PROX_CV | Proximity Index (Coefficient of variation) |
| | H1 - Climate & Topography | Slope_MN | Slope (mean value for the 1km2 square (%) |

| | | | |
|---|---|---|---|
| **Estimated number of shrublands specialist species** | | Slope_SD | Slope (standard deviation) |
| | H2 - Habitat diversity | h_habitats | Shannon index of habitat types |
| | H3 - Habitat disturbance | BurntPercMN_03_12 | Average 2003 - 2012 burnt area percentage (%) |
| | H4 - Landscape composition | built_up_areas | Cover of built up areas (m) |
| | | permanent_crops | Cover of permanent crops (m) |
| | H5 - Landscape structure | GYRATE_RA | Radius of Gyration (Range) |
| | | CONTIG_SD | Contiguity Index (Standard deviation) |
| | | SPLIT | Splitting Index |
| **Estimated number of woodlands specialist species** | H1 - Climate & Topography | BIO_15 | Precipitation seasonality (coefficient of variation) (mm) |
| | | BIO_16 | Precipitation of wettest quarter (mm) |
| | H2 - Habitat diversity | hab_richness | Habitat richness |
| | | sp_richplant | Plant species richness |
| | H3 - Habitat disturbance | COS90_12_Cat_Change | Cover of areas that changed the land cover/use category between 1990-2012 |
| | H4 - Landscape composition | natural_forest | Cover of natural forest (m) |
| | | production_forest | Cover of production forest (m) |
| | H5 - Landscape structure | CORE_AM | Core Area (Area weighted mean) |
| | | PROX_CV | Proximity Index (Coefficient of variation) |

## Appendix III. Hierarchical cluster analysis data

**(a)** Euclidean distance matrix based on Akaike weights obtained from the multi-model inference (MMI) analysis in step 5, used in the hierarchical cluster analysis.

| | **H0 – Null hypothesis** | **H1 – Climate & Topography** | **H2 – Habitat diversity** | **H3 –Habitat disturbance** | **H4 – Landscape composition** | **H5 – Landscape structure** |
|---|---|---|---|---|---|---|
| **Feeding.G.multiSAR** | 1.05E-07 | 0.000462 | 5.63E-08 | 0.331776 | 1.34E-05 | 0.667748 |
| **Feeding.I.multiSAR** | 0.000846 | 0.026029 | 0.382572 | 0.029298 | 0.470964 | 0.090291 |
| **Feeding.O.multiSAR** | 1.89E-10 | 0.000711 | 0.000806 | 5.24E-10 | 0.000276 | 0.998207 |
| **Foraging.O.multiSAR** | 1.11E-07 | 0.001250 | 0.000124 | 3.90E-06 | 0.001281 | 0.997341 |
| **Foraging.S.multiSAR** | 1.98E-06 | 0.179257 | 2.05E-06 | 5.05E-05 | 0.100168 | 0.720520 |
| **SpRich.multiSAR** | 8.74E-07 | 0.005191 | 0.029454 | 0.001142 | 0.048489 | 0.915723 |
| **Foraging.W.multiSAR** | 0.000119 | 0.329872 | 0.577537 | 0.011945 | 0.023287 | 0.057239 |

**(b)** Distance matrix based on 1 – Spearman Correlation between the responses variables, used in the hierarchical cluster analysis.

| | **SpRich.multiSAR** | **Foraging.W.multiSAR** | **Foraging.O.multiSAR** | **Foraging.S.multiSAR** | **Feeding.I.multiSAR** | **Feeding.G.multiSAR** | **Feeding.O.multiSAR** |
|---|---|---|---|---|---|---|---|
| **SpRich.multiSAR** | 1 | 0.64 | 0.86 | 0.34 | 0.78 | 0.81 | 0.44 |
| **Foraging.W.multiSAR** | 0.64 | 1 | 0.48 | -0.06 | 0.6 | 0.38 | 0.34 |
| **Foraging.O.multiSAR** | 0.86 | 0.48 | 1 | 0.22 | 0.79 | 0.72 | 0.45 |
| **Foraging.S.multiSAR** | 0.34 | -0.06 | 0.22 | 1 | 0.23 | 0.52 | -0.09 |
| **Feeding.I.multiSAR** | 0.78 | 0.6 | 0.79 | 0.23 | 1 | 0.56 | 0.34 |
| **Feeding.G.multiSAR** | 0.81 | 0.38 | 0.72 | 0.52 | 0.56 | 1 | 0.18 |
| **Feeding.O.multiSAR** | 0.44 | 0.34 | 0.45 | -0.09 | 0.34 | 0.18 | 1 |

**Appendix IV. List of passerine species recorded**

List of passerine species recorded along the catchment of medium-sized river Vez in the Northwest of Portugal during spring of 2014. Classification of feeding habits and foraging habitats follows Catry et al. (2010) and Moreira et al. (2001a), respectively.

| Family | Species name | Order | Foraging habitat | Feeding habit |
|---|---|---|---|---|
| Aegithalidae | *Aegithalos caudatus* | Passeriformes | Shrubland | Insectivore |
| Alaudidae | *Alauda arvensis* | Passeriformes | Open Area | Granivore |
| Certhiidae | *Certhia brachydactyla* | Passeriformes | Woodland | Insectivore |
| Cettiidae | *Cettia cetti* | Passeriformes | Shrubland | Insectivore |
| Corvidae | *Corvus corax* | Passeriformes | Open Area | Omnivore |
| Corvidae | *Corvus corone* | Passeriformes | Open Area | Omnivore |
| Corvidae | *Corvus monedula* | Passeriformes | Open Area | Omnivore |
| Corvidae | *Corvus sp.** | Passeriformes | Open Area | Omnivore |
| Corvidae | *Garrulus glandarius* | Passeriformes | Woodland | Omnivore |
| Corvidae | *Pica pica* | Passeriformes | Open Area | Omnivore |
| Emberizidae | *Emberiza cia* | Passeriformes | Open Area | Granivore |
| Emberizidae | *Emberiza cirlus* | Passeriformes | Shrubland | Granivore |
| Emberizidae | *Emberiza citrinella* | Passeriformes | Open Area | Granivore |
| Emberizidae | *Emberiza sp.** | Passeriformes | Open Area | Granivore |
| Fringillidae | *Carduelis cannabina* | Passeriformes | Shrubland | Granivore |
| Fringillidae | *Carduelis carduelis* | Passeriformes | Open Area | Granivore |
| Fringillidae | *Carduelis chloris* | Passeriformes | Open Area | Granivore |
| Fringillidae | *Carduelis sp.** | Passeriformes | Open Area | Granivore |
| Fringillidae | *Fringilla coelebs* | Passeriformes | Woodland | Omnivore |
| Fringillidae | *Pyrrhula pyrrhula* | Passeriformes | Woodland | Granivore |
| Fringillidae | *Serinus serinus* | Passeriformes | Open Area | Granivore |
| Hirundinidae | *Delichon urbicum* | Passeriformes | Open Area | Insectivore |
| Hirundinidae | *Hirundo rustica* | Passeriformes | Open Area | Insectivore |
| Hirundinidae | *Hirundo sp.** | Passeriformes | Open Area | Insectivore |
| Motacillidae | *Anthus sp.** | Passeriformes | Open Area | Insectivore |
| Motacillidae | *Anthus trivialis* | Passeriformes | Open Area | Insectivore |
| Muscicapidae | *Erithacus rubecula* | Passeriformes | Woodland | Insectivore |
| Muscicapidae | *Luscinia megarhynchos* | Passeriformes | Shrubland | Insectivore |
| Muscicapidae | *Monticola sp.** | Passeriformes | Open Area | Insectivore |
| Muscicapidae | *Oenanthe oenanthe* | Passeriformes | Open Area | Insectivore |

* During survey, a complete identification was not possible, thus, only the genus was registered.

(Continued)

| Family | Species name | Order | Foraging habitat | Feeding habit |
|---|---|---|---|---|
| Muscicapidae | *Oenanthe sp.** | Passeriformes | Open Area | Insectivore |
| Muscicapidae | *Saxicola rubetra* | Passeriformes | Open Area | Insectivore |
| Muscicapidae | *Saxicola torquata* | Passeriformes | Open Area | Insectivore |
| Oriolidae | *Oriolus oriolus* | Passeriformes | Woodland | Insectivore |
| Paridae | *Parus ater* | Passeriformes | Woodland | Insectivore |
| Paridae | *Parus caeruleus* | Passeriformes | Woodland | Insectivore |
| Paridae | *Parus cristatus* | Passeriformes | Woodland | Insectivore |
| Paridae | *Parus major* | Passeriformes | Woodland | Insectivore |
| Paridae | *Parus sp.** | Passeriformes | Woodland | Insectivore |
| Passeridae | *Motacilla alba* | Passeriformes | Open Area | Insectivore |
| Passeridae | *Motacilla cinerea* | Passeriformes | Open Area | Insectivore |
| Passeridae | *Passer domesticus* | Passeriformes | Open Area | Granivore |
| Passeridae | *Passer montanus* | Passeriformes | Open Area | Granivore |
| Phylloscopidae | *Phylloscopus sp.** | Passeriformes | Woodland | Insectivore |
| Prunellidae | *Prunella modularis* | Passeriformes | Shrubland | Insectivore |
| Regulidae | *Regulus ignicapillus* | Passeriformes | Woodland | Insectivore |
| Sittidae | *Sitta europaea* | Passeriformes | Woodland | Insectivore |
| Sturnidae | *Sturnus unicolor* | Passeriformes | Open Area | Omnivore |
| Sylviidae | *Hippolais polyglotta* | Passeriformes | Shrubland | Insectivore |
| Sylviidae | *Sylvia atricapilla* | Passeriformes | Woodland | Insectivore |
| Sylviidae | *Sylvia cantillans* | Passeriformes | Shrubland | Insectivore |
| Sylviidae | *Sylvia communis* | Passeriformes | Shrubland | Insectivore |
| Sylviidae | *Sylvia melanocephala* | Passeriformes | Shrubland | Insectivore |
| Sylviidae | *Sylvia sp.** | Passeriformes | Shrubland | Insectivore |
| Sylviidae | *Sylvia undata* | Passeriformes | Shrubland | Insectivore |
| Troglodytidae | *Troglodytes troglodytes* | Passeriformes | Woodland | Insectivore |
| Turdidae | *Phoenicurus ochruros* | Passeriformes | Open Area | Insectivore |
| Turdidae | *Turdus merula* | Passeriformes | Woodland | Omnivore |
| Turdidae | *Turdus philomelos* | Passeriformes | Woodland | Omnivore |
| Turdidae | *Turdus sp.** | Passeriformes | Woodland | Omnivore |
| Turdidae | *Turdus viscivorus* | Passeriformes | Woodland | Omnivore |

* During survey, a complete identification was not possible, thus, only the genus was registered.

## Appendix V. Species richness data

Summary table of observed species richness data recorded along the catchment of medium-sized river Vez in the Northwest of Portugal during spring of 2014 and SAR-estimated species richness data.

| | Code name | Variables Description | Mean | Min | Máx |
|---|---|---|---|---|---|
| **Observed species richness** | SpRich.ObsField | Observed passerine species richness | 18 | 9 | 26 |
| | Feeding.I.ObsField | Observed number of insectivorous species | 11 | 5 | 17 |
| | Feeding.G.ObsField | Observed number of granivorous species | 5 | 2 | 9 |
| | Feeding.O.ObsField | Observed number of omnivorous species | 1 | 0 | 3 |
| | Foraging.O.ObsField | Observed number of open areas specialist species | 7 | 2 | 12 |
| | Foraging.S.ObsField | Observed number of shrublands specialist species | 2 | 0 | 7 |
| | Foraging.W.ObsField | Observed number of woodlands specialist species | 8 | 1 | 11 |
| **Estimated species richness (SAR)** | SpRich.multiSAR | Estimated passerine species richness | 31 | 12 | 51 |
| | Feeding.I.multiSAR | Estimated number of insectivorous species | 21 | 7 | 32 |
| | Feeding.G.multiSAR | Estimated number of granivorous species | 10 | 4 | 28 |
| | Feeding.O.multiSAR | Estimated number of omnivorous species | 3 | 0 | 9 |
| | Foraging.O.multiSAR | Estimated number of open areas specialist species | 15 | 4 | 29 |
| | Foraging.S.multiSAR | Estimated number of shrublands specialist species | 5 | 0 | 12 |
| | Foraging.W.multiSAR | Estimated number of woodlands specialist species | 14 | 2 | 22 |

## Appendix VI. Landscape metrics description

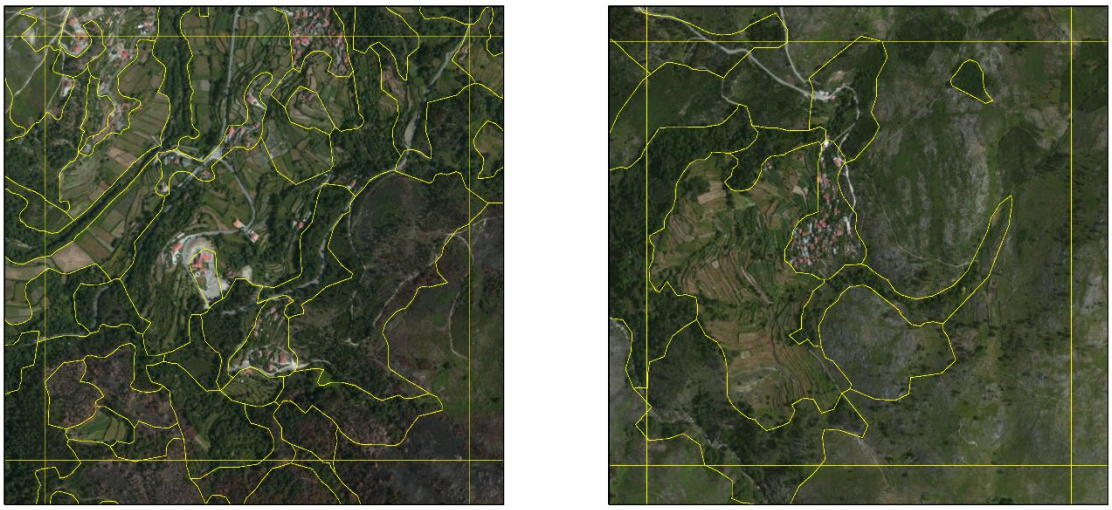
Description of each landscape metric selected in the best MMI models based on estimated species richness variables, taken from the Fragstats 4.2 software user manual (McGarigal et al., 2012). Example images are representative from the study area and were obtained using ESRI service layer in ArcGIS 10.1 software (ESRI, Redlands, CA).

**AREA_RA – Range of Patch Area**

Low AREA_RA (8.26) → High AREA_RA (74.15)

| | |
|---|---|
| Formula | $AREA = a_{ij}\left(\frac{1}{10{,}000}\right)$ aij = area (m2) of patch ij |
| Description | AREA equals the area (m2) of the patch, divided by 10,000 (to convert to hectares); Units: Hectares. |
| Range | AREA > 0, without limit.<br>The range in AREA is limited by the grain and extent of the image; in a particular application, AREA may be further limited by the specification of a minimum patch size that is larger than the grain. |
| Comments | The area of each patch comprising a landscape mosaic is perhaps the single most important and useful piece of information contained in the landscape. Not only is this information the basis for many of the patch, class, and landscape indices, but patch area has a great deal of ecological utility in its own right. Note that the choice of the 4-neighbor or 8-neighbor rule for delineating patches will have an impact on this metric |
| | $RA = x_{max} - x_{min}$ RA (range) equals the value of the corresponding patch metric for the largest observed value minus the smallest observed value (i.e., the difference between the maximum and minimum observed values) for all patches in the landscape. |

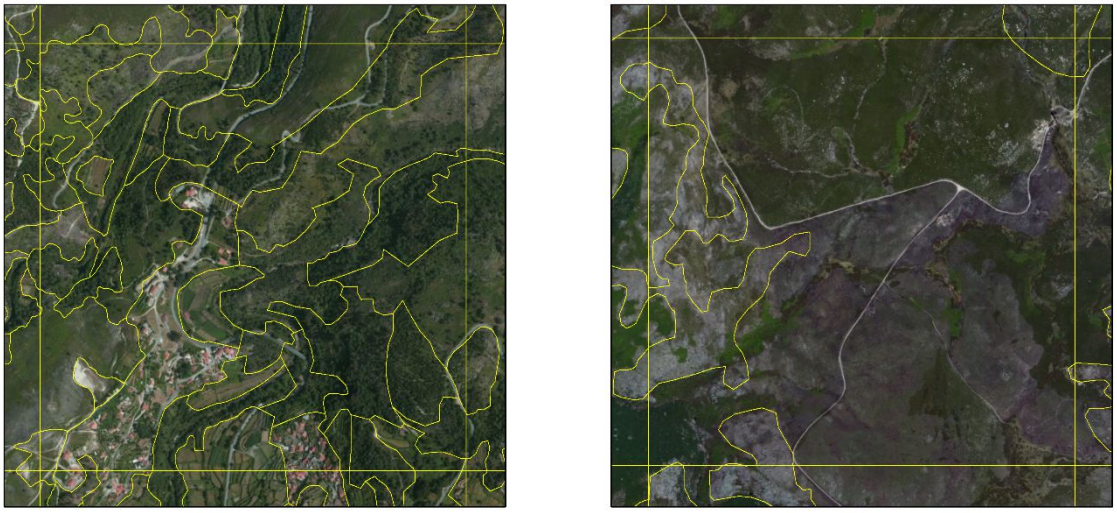
**CONTIG_SD – Standard deviation of Contiguity Index**



Low CONTIG_SD (0.0705) ⟶ High CONTIG_SD (0.3241)

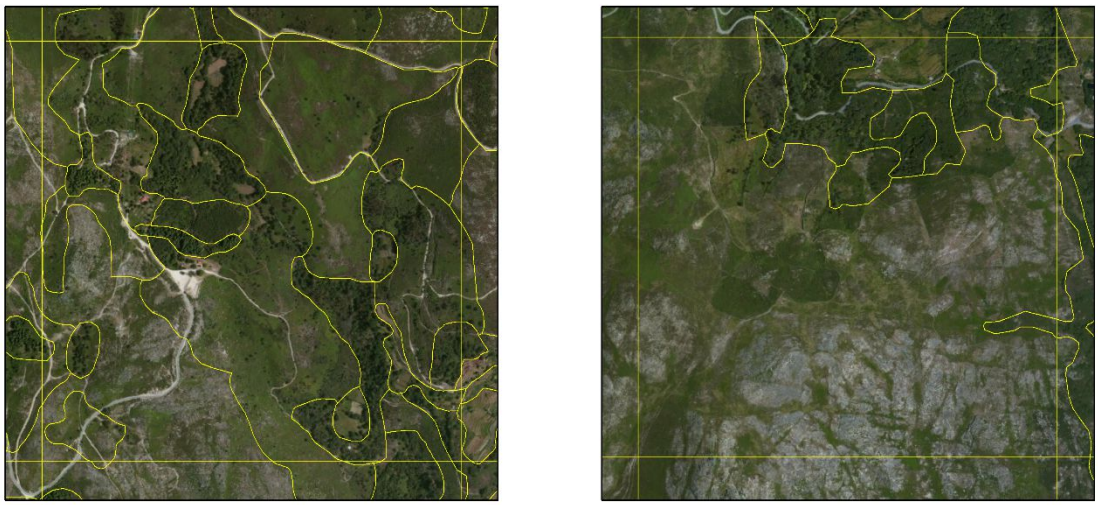
| | |
|---|---|
| Formula | $CONTIG = \frac{\left[\frac{\sum_{r=1}^{z} c_{ijr}}{a_{ij}^{*}}\right] - 1}{v-1}$<br>cijr = contiguity value for pixel r in patch ij.<br>v = sum of the values in a 3-by-3 cell template (13 in this case).<br>aij* = area of patch ij in terms of number of cells. |
| Description | CONTIG equals the average contiguity value (see discussion) for the cells in a patch (i.e., sum of the cell values divided by the total number of pixels in the patch) minus 1, divided by the sum of the template values (13 in this case) minus 1. |
| Range | 0 ≦ CONTIG ≦ 1<br>CONTIG equals 0 for a one-pixel patch and increases to a limit of 1 as patch contiguity, or connectedness, increases. Note, 1 is subtracted from both the numerator and denominator to confine the index to a range of 1. |
| Comments | Contiguity index assesses the spatial connectedness, or contiguity, of cells within a grid-cell patch to provide an index on patch boundary configuration and thus patch shape (LaGro 1991). |
| | $SD = \sqrt{\frac{\sum_{i=1}^{m}\sum_{j=1}^{n}\left[x_{ij} - \left(\frac{\sum_{i=1}^{m}\sum_{j=1}^{n} x_{ij}}{N}\right)\right]^2}{N}}$<br>SD (standard deviation) equals the square root of the sum of the squared deviations of each patch metric value from the mean metric value computed for all patches in the landscape, divided by the total number of patches; that is, the root mean squared error (deviation from the mean) in the corresponding patch metric. Note, this is the population standard deviation, not the sample standard deviation. |

**CORE_AM – Area-weighted mean of Core area**




| | |
|---|---|
| Formula | aijc = core area (m2) of patch ij based on specified edge depths (m).<br>$TCA = \sum_{i=1}^{m}\sum_{j=1}^{n} a_{ij}^{c}\left(\frac{1}{10{,}000}\right)$ |
| Description | TCA equals the sum of the core areas of each patch (m2), divided by 10,000 (to convert to hectares). |
| Range | TCA ≥ 0, without limit.<br>TCA = 0 when every location within every patch is within the specified depth-of-edge distance(s) from the patch perimeters. TCA approaches total landscape area as the specified depth-of-edge distance(s) decreases and as patch shapes are simplified. |
| Comments | Total core area is defined the same as Core area (CORE) at the patch level (see Core Area), but here core area is aggregated (summed) over all patches. |
| | $AM = \sum_{i=1}^{m}\sum_{j=1}^{n}\left[x_{ij}\left(\frac{a_{ij}}{\sum_{i=1}^{m}\sum_{j=1}^{n} a_{ij}}\right)\right]$<br>AM (area-weighted mean) equals the sum, across all patches in the landscape, of the corresponding patch metric value multiplied by the proportional abundance of the patch [i.e., patch area ($m^2$) divided by the sum of patch areas]. Note, the proportional abundance of each patch is determined from the sum of patch areas rather than the total landscape area, because the latter may include internal background area not associated with any patch. |

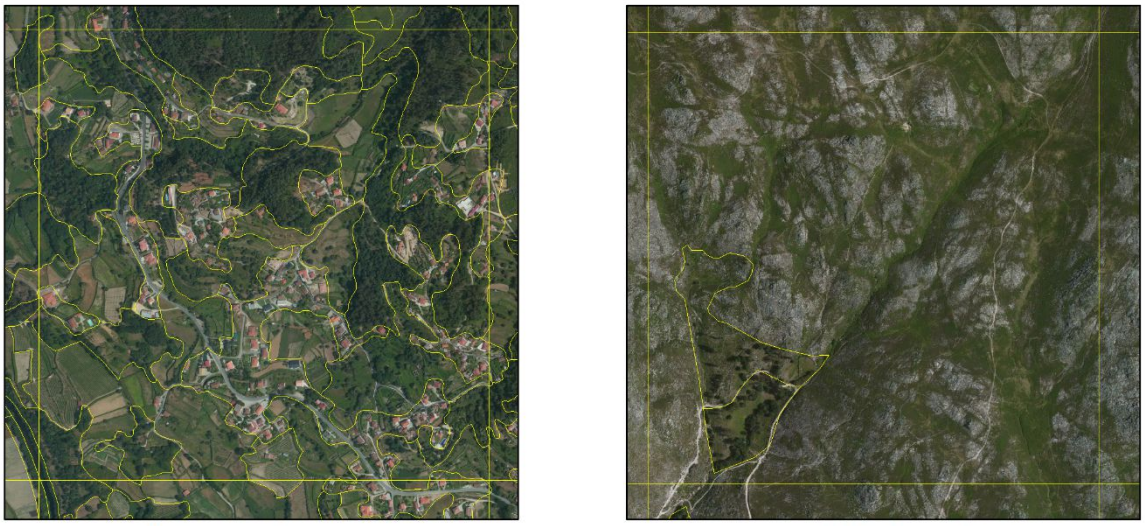
**GYRATE_RA – Range of Radius of Gyration**



Low GYRATE_RA (108.4075) ⟶ High GYRATE_RA (342.1413)

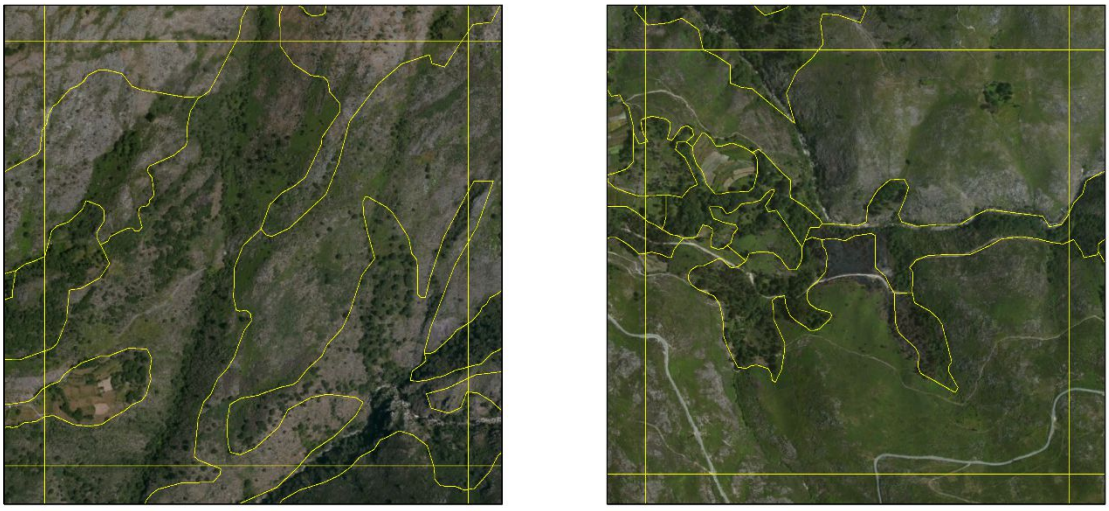
| | | |
|---|---|---|
| Formula | $GYRATE = \sum_{r=1}^{z} \frac{h_{ijr}}{z}$ | hijr = distance (m) between cell ijr [located within patch ij] and the centroid of patch ij (the average location), based on cell center-to-cell center distance.<br>z = number of cells in patch ij. |
| Description | GYRATE equals the mean distance (m) between each cell in the patch and the patch centroid. | |
| Range | GYRATE ≥ 0, without limit.<br>GYRATE = 0 when the patch consists of a single cell and increases without limit as the patch increases in extent. GYRATE achieves its maximum value when the patch comprises the entire landscape. | |
| Comments | Radius of gyration is a measure of patch extent (i.e., how far-reaching it is); thus, it is effected by both patch size and patch compaction. Note that the choice of the 4-neighbor or 8-neighbor rule for delineating patches will have an impact on this metric. | |
| | $RA = x_{max} - x_{min}$ | RA (range) equals the value of the corresponding patch metric for the largest observed value minus the smallest observed value (i.e., the difference between the maximum and minimum observed values) for all patches in the landscape. |

**MESH – Effective Mesh Size**




| | |
|---|---|
| Formula | $MESH = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n} a_{ij}^{2}}{A}$ <br> aij = area (m2) of patch ij. <br> A = total landscape area (m2). |
| Description | MESH equals 1 divided by the total landscape area (m2) multiplied by the sum of patch area (m2) squared, summed across all patches in the landscape. Note, total landscape area (A) includes any internal background present. Units: Hectares. |
| Range | cell size ≦ MESH ≦ total landscape area (A) <br> The lower limit of MESH is constrained by the cell size and is achieved when the landscape is maximally subdivided; that is, when every cell is a separate patch. MESH is maximum when the landscape consists of a single patch. |
| Comments | Mesh is based on the cumulative patch area distribution and is interpreted as the size of the patches when the landscape is subdivided into S patches, where S is the value of the splitting index. Note, MESH is redundant with DIVISION above, i.e., they are perfectly, but inversely, correlated, but both metrics are included because of differences in units and interpretation. DIVISION is interpreted as a probability, whereas MESH is given as an area. In addition, note the similarity between MESH and Area-weight mean patch size (AREA_AM). Conceptually and computationally, these two metrics are almost identical at the landscape level, and under most circumstances will return identical values. Specifically, AREA_AM gives the area-weight mean patch size, where the proportional area of each patch is based on total landscape area excluding any background (i.e., background is excluded from the total landscape area). MESH also gives the area-weighted mean patch size, but the proportional area of each patch is based on the total landscape area including any background. Background is included in the so-called 'pedestal' of Jaeger (2000). Thus, if there is no internal background, these metrics will return identical values. If there is internal background, these metrics will return different values, and the magnitude of the difference will depend on the proportional extent of background. In the latter case, the choice of metrics depends on how you want to consider background. |

**PARA_RA – Range of Perimeter-Area ratio**



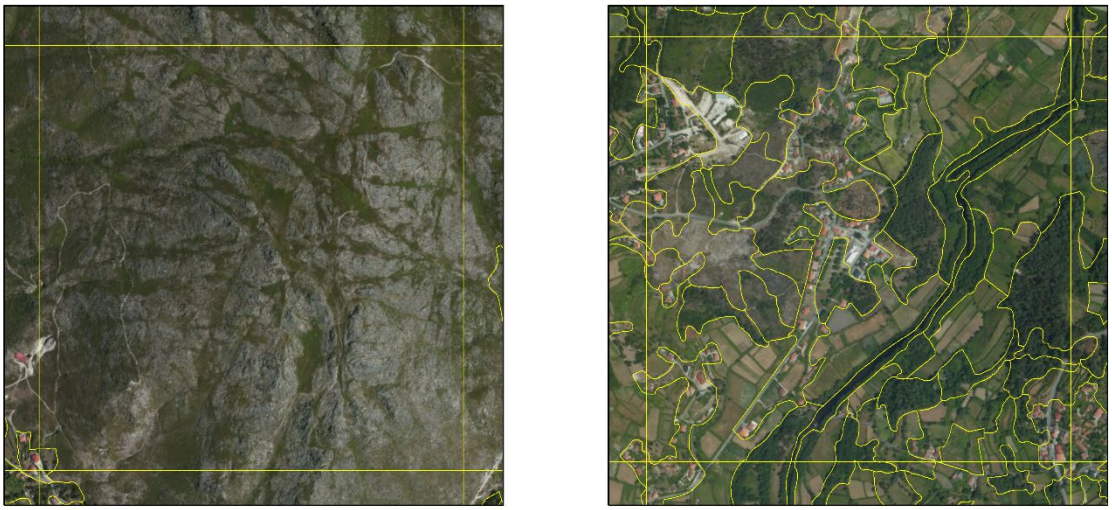
Low PARA_RA (599.4602) → High PARA_RA (3879.26)

| | |
|---|---|
| Formula | pij = perimeter (m) of patch ij. aij = area (m2) of patch ij. $PARA = \frac{p_{ij}}{a_{ij}}$ |
| Description | PARA equals the ratio of the patch perimeter (m) to area (m2). |
| Range | PARA > 0, without limit. |
| Comments | Perimeter-area ratio is a simple measure of shape complexity, but without standardization to a simple Euclidean shape (e.g., square). A problem with this metric as a shape index is that it varies with the size of the patch. For example, holding shape constant, an increase in patch size will cause a decrease in the perimeter-area ratio. |
| | $RA = x_{max} - x_{min}$ RA (range) equals the value of the corresponding patch metric for the largest observed value minus the smallest observed value (i.e., the difference between the maximum and minimum observed values) for all patches in the landscape. |

## PROX_CV – Coefficient of variation of Proximity Index


| | |
|---|---|
| Formula | $PROX = \sum_{s=1}^{n} \frac{a_{ijs}}{h_{ijs}^2}$<br>aijs = area (m2) of patch ijs within specified neighborhood (m) of patch ij.<br>hijs = distance (m) between patch ijs and patch ijs, based on patch edge-to-edge distance, computed from cell center to cell center. |
| Description | PROX equals the sum of patch area (m2) divided by the nearest edge-to-edge distance squared (m2) between the patch and the focal patch of all patches of the corresponding patch type whose edges are within a specified distance (m) of the focal patch. Note, when the search buffer extends beyond the landscape boundary, only patches contained within the landscape are considered in the computations. In addition, note that the edge-to-edge distances are from cell center to cell center. |
| Range | PROX ≥ 0.<br><br>PROX = 0 if a patch has no neighbors of the same patch type within the specified search radius. PROX increases as the neighborhood (defined by the specified search radius) is increasingly occupied by patches of the same type and as those patches become closer and more contiguous (or less fragmented) in distribution. The upper limit of PROX is affected by the search radius and the minimum distance between patches. |
| Comments | Proximity index was developed by Gustafson and Parker (1992) and considers the size and proximity of all patches whose edges are within a specified search radius of the focal patch. Note that FRAGSTATS uses the distance between the focal patch and each of the other patches within the search radius, similar to the isolation index of Whitcomb et al. (1981), rather than the nearest-neighbor distance of each patch within the search radius (which could be to a patch other than the focal patch), as in Gustafson and Parker (1992). The index is dimensionless (i.e., has no units) and therefore the absolute value of the index has little interpretive value; instead it is used as a comparative index. |
| | $CV = \frac{SD}{MN}(100)$<br>CV (coefficient of variation) equals the standard deviation divided by the mean, multiplied by 100 to convert to a percentage, for the corresponding patch metric. |

## SPLIT – Splitting Index



Low SLPIT index (1.0042) ⟶ High SPLIT index (23.0924)

| | |
|---|---|
| Formula | $$SPLIT = \frac{A^2}{\sum_{i=1}^{m}\sum_{j=1}^{n} a_{ij}^2}$$ aij = area (m2) of patch ij.<br>A = total landscape area (m2). |
| Description | SPLIT equals the total landscape area (m2) squared divided by the sum of patch area (m2) squared, summed across all patches in the landscape. Note, total landscape area (A) includes any internal background present. |
| Range | 1 ≦ SPLIT ≦ number of cells in the landscape squared<br><br>SPLIT = 1 when the landscape consists of single patch. SPLIT increases as the landscape is increasingly subdivided into smaller patches and achieves its maximum value when the landscape is maximally subdivided; that is, when every cell is a separate patch. |
| Comments | Split is based on the cumulative patch area distribution and is interpreted as the effective mesh number, or number of patches with a constant patch size when the landscape is subdivided into S patches, where S is the value of the splitting index. |